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MODES OF BEHAVIORAL ADAPTATION IN CHIMPANZEE TO MULTIPLE-CHOICE PROBLEMS

BY

ROBERT M. YERKES
Yale University

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MODES OF BEHAVIORAL ADAPTATION IN CHIMPANZEE TO MULTIPLE-CHOICE PROBLEMS

ROBERT M. YERKES

Laboratories of Comparative Psychobiology, Yale University

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HISTORICAL SETTING OF INVESTIGATION

This report is a long-delayed sequel to a study of "ideational behavior" in monkeys and apes which I published in *Behavior Monographs* in 1916. At that time I planned to proceed at once with the application of my "method of multiple choices" to other primates. The World War intervened, and it was several years before suitable opportunity offered for the resumption of my investigation. Thrice in the past eight years I have attempted to present relational problems to chimpanzee subjects by the multiple-choice method, but each time until the last I met conditions or results which contra-indicated continuance. Difficulties arose primarily from my desire to simplify apparatus and procedure by utilization of a manual device, while persevering in the use of the problems which had previously been presented to crows, doves, rats, pigs, monkeys, orang-outan, and both normal and abnormal men. Had I chosen to sacrifice comparability of results and simplify markedly both problems and apparatus, progress doubtless would have been facilitated. Finally, some two years ago, I decided to revert to my original box apparatus, as used for monkey and orang-outan in the California laboratory of my friend Doctor G. V. Hamilton, and to proceed with a study of multiple-choice responses in chimpanzee.[1]

The method of multiple choice involves the presentation successively to a subject of groups of identical response mechanisms (open boxes, in this instance), among which some one mechanism, if operated, will yield success. The number of mechanisms in a group and their position in the apparatus are variable, and the correct mechanism may be defined only in terms of its spatial relations to the other members of the group; as, for example, by middleness or left-endedness. Problem 6 of this report is an exception to this rule, in that the same numbered mechanism was correct, whatever the group of mechanisms in use.

This investigation was not directed to the solution of a single problem, but instead was conducted as an exploratory inquiry to exhibit characteristics of chimpanzee behavior and to provide the basis for intelligent formulation of problems. In the investigator's mind, however, were such research interests as desire to discover the nature and conditions of sudden behavioral adaptations, if and when exhibited; to discover methods of response (reactive tendencies of Hamilton, 1916) of chimpanzee to a given problematic situation, and response patterns as described by Yerkes (1916) and Krechevsky (1932); to determine, from prior response and the history of a subject's behavior, degree of predictability of success in solving relational problems; the serviceability of positive and negative motivational factors, and optimal

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[1] Doctor Kenneth W. Spence, in these laboratories, is now engaged in an attempt to evaluate the manual form of multiple-choice apparatus, and to discover modifications of procedure and apparatus which will increase the efficiency of the method and enhance the value of its results.

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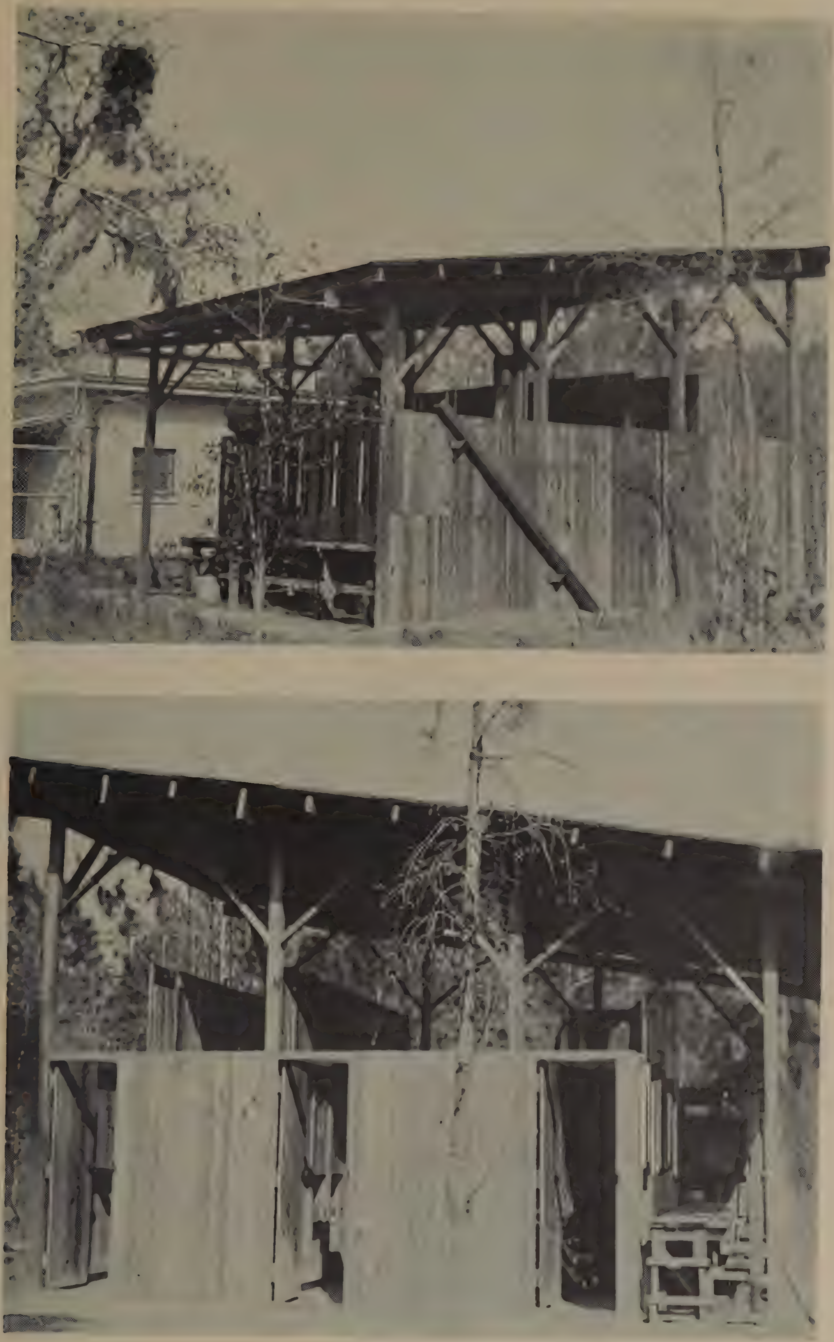

Fig. 1. Upper: Multiple-choice apparatus seen from front. Food chute on side wall. Entrance and exit doors of boxes raised. Lower: Apparatus seen from side, with all box doors raised and doors to *A*, *B*, and *C* of figure 2 open.

conditions of response; and, finally, relations of success or failure in adaptation to the affectivity and docility of the subject.

The multiple-choice method was devised originally to exhibit reactive tendencies, modes of behavioral adaptation, conditions and relations thereof, which may be characteristic of certain types of organism, certain individuals, certain developmental stages or conditions.

APPARATUS AND PROCEDURE

The apparatus for this study of chimpanzee in principle duplicated that previously used in California. In this case it was located out-of-doors at the Yale Anthropoid Experiment Station, Orange Park, Florida, in convenient proximity to the animal quarters. A roof was provided for protection from sun and rain. The external appearance of the apparatus as housed is exhibited in figure 1; the floor plan and relationship of parts, by figure 2, and the door-locking mechanism by figure 3.

The following description of apparatus and method of use presupposes knowledge of the content of *Behavior Monographs*, vol. 3, no. 1. Effort has been made, however, to render it complete and independently intelligible. Functionally important parts of the apparatus are described by title in the legend of figure 2, and all essential dimensions are presented.

Hinged doors at *a*, *c*, and *d* give access to the three important divisions of the apparatus. The entrance alley is divided by slide door *z* into sections *A* and *E*, in order that two subjects may be used in company, although separately. Entrance and exit doors for the boxes numbered 1 to 9 are raised and lowered by means of a system of counterweighted cords, and the slide doors *x*, *y*, and *z* are similarly operated. Another system of cords, in accordance with the principles diagrammatically represented in figure 3, operates locks, which when engaged prevent the entrance door, exit door, or both, of a given box from being raised.

The Florida form of box multiple-choice apparatus, aside from minor differences of dimensions and design of parts, differs from the California apparatus in that it has one instead of two return alleys (*D*) and a food chute (*h*), which enabled the experimenter

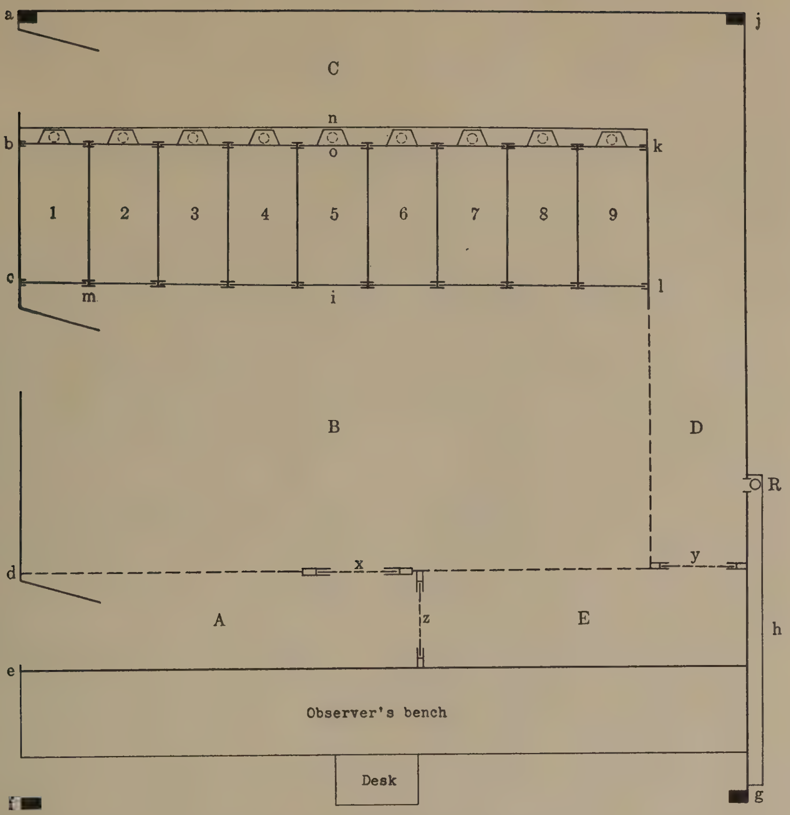

FIG. 2. GROUND PLAN OF MULTIPLE-CHOICE APPARATUS. SCALE ABOUT 1:50.
LEGEND AND ESSENTIAL DIMENSIONS

A, entrance alley; *B*, response compartment; *C*, exit alley; *D*, return alley; *E*, waiting room; *1–9*, reaction boxes, numbered left to right; *i*, entrance door of box; *o*, exit door of box; *n*, metal cover plate over food cup, which is dotted in; *x*, door, *A* to *B*; *y*, door, *D* to *E*; *z*, door, *E* to *A*; *a*, *c*, *d*, hinged doors for access to apparatus; *h*, food chute; *R*, food container, accessible to animal from alley *D*. Drawing by P. E. Nelbach.

Dimensions, in centimeters. *Apparatus as whole.* Length, *a–f*, 575; width, *a–j*, 525; width between corner posts, 500; height to wire-mesh (19 gauge, 3 mesh to inch) ceiling, 190; ground to roof at *a–j* (rear of apparatus), 200; ground to roof at *f–g* (front of apparatus), 100.

Alleys. Width *A*, *D*, *E*, 70; width *C*, 85; height, *A*, *C*, *D*, *E*, ground to ceiling, 190; partitions between *A*, *E*, *D*, and *B*, 2-inch mesh, 11 gauge wire-link netting.

Response compartment B. Length, *c–d*, 210; width, *c–l*, 440; height, 190.

Observer's bench. 525 x 65; 70 from ground.

Reaction boxes. Total width of *1–9*, 440; length of box, *b–c*, 100; width, *c–m*, 45; wooden floor of box 30 from ground; height, floor to wire ceiling, 165.

Doors. Hinged doors at *a*, *c*, *d*, 60 x 180 x 2.3; lock set 90 from bottom of door. Entrance doors of boxes each 44 x 165; window in door 20 from bottom of door, 17 wide by 45 high, opening covered with 19 gauge, 3-mesh-per-inch wire netting. Exit doors of boxes, each 44 x 165; metal cover plate, *n*, for food cup, bolted to entrance door near bottom, plate 30 at attachment to door, 20 at outer edge, 18 from door to edge; hole for aluminum food cup 10 diameter by 6 deep. All doors operated by window-cord-pulley system, with cast lead counterweights 70 x 4, weighing about 9 kgm. Doors between alleys or compartments: *x*, 58 x 180, opening, 55 x 180; *y* and *z*, each 50 x 180. These three doors consisted of light wooden frame carrying 19 gauge, 3-mesh-to-inch wire netting. Floor of apparatus, except in reaction boxes, lime-rock, with covering of sand.

to present rewards at *R*. As appears in figure 2, food as reward for effort could be offered either in a food cup just outside the exit door of a given box or at *R* in alley *D*.

In general, procedure of experimentation involved the following steps. Supply of food was provided either in the box food cups or for use at *R*. The subject was brought from its quarters to alley *A*. The experimenter raised to a standard height of 70 cm. the entrance doors of a given group of boxes. For the first problem in this investigation the initial setting of doors included boxes 1, 2, 3. The subject, which previously had discovered that a reward could be obtained by passing through one of the open boxes, was next admitted to *B* and the door *x* was lowered. The animal now was confronted by three open box doors, of which by definition the one at the left end of the group was correct. It might enter any one of boxes 1 to 3, but only upon entering box 1 was the corresponding exit door raised and reward offered for completion of the trial. The exit door was closed regularly after the subject had passed into alley *C*. As soon as the observer had completed his record of the trial, slide door *y* was momentarily raised to permit the animal to return to *E*,

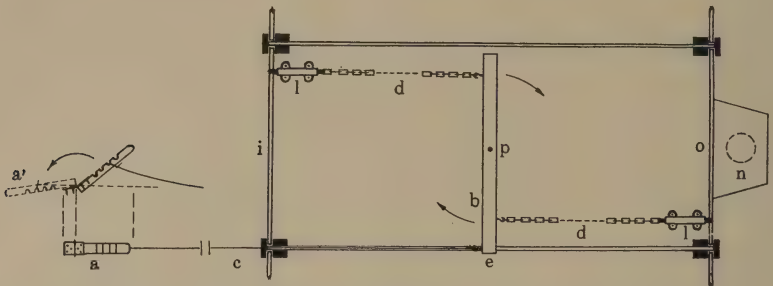

Fig. 3. Locking System for Doors of Boxes *1–9* of Figure 2. Scale 1:17

The figure represents the system (diagrammatically) as it appears from above the box. The wire netting ceiling of the box is not represented. Symbols: *b*, iron bar to function as lever, pivoted at *p*, with cord *c* attached at *e*; *l*, *l*, spring window-bolt locks, whose bolts when extended engaged the tops of doors *i* and *o*; *d*, chain connecting *b* with *l*. Cord *c* extended from lever *b* to the partition between the observer's bench and alley *A–E* of figure 2, where it terminated in an oak lever, *a*, which was hinged to the partition at one end. When this lever was upright, *a*, the doors of a box were locked; when it was pulled back into horizontal position, *a′*, they were unlocked. Drawing by P. E. Nelbach.

where it waited in readiness for the next trial. When an animal was used alone in the apparatus, door *z* was open continuously and spaces *A* and *E* were used as a single compartment; but when two subjects were used in company, the one was held in *E* while the other, starting from *A*, responded to a setting of the doors.

The following terms and abbreviations used throughout this report require formal definition: *trial* designates response to a given setting of the doors of the multiple-choice apparatus; *setting* designates the group of box doors open for a given trial; *series* designates ten prearranged settings, as exhibited in table 1. Where the abbreviation O is used, it designates observer or experimenter, and, similarly, S refers to the animal subject.

Unless otherwise stated, the regular series of ten settings was presented to a subject daily, without interruption. This procedure was continued, the same settings being used each day, until the subject responded correctly by initial choice in each of the ten trials of the series. Thereupon, having met the arbitrary criterion for solution of the problem, it was confronted, on the next day, with the ten settings of a different series which is designated as control series.

Originally the standard procedure for the control series varied from that of the regular series in that only one choice (response) was permitted in a trial and S was allowed to pass through the selected box, whether or not correct, and given food. This procedure evidently placed a premium upon carelessness. Therefore, in several instances, which are either specifically mentioned in the text or indicated in the tables by excess of responses over ten, the procedure was varied by requiring S to continue to choose until the correct box had been selected.

Six relational problems, as presented to each of four young chimpanzees, supplied the observational data for this report. They are describable in terms of the reward-yielding or correct reaction mechanism as: problem 1, the left-end box, in any group of open boxes; problem 2, the box second from the right end; problem 3, the right-end box; problem 4, the middle box; problem 5, alternately the left-end and the right-end box, the group remaining constant for two successive settings; and problem 6, the same box, no. 5, whichever doors were open.

For each of these six relational problems a regular series of ten settings of the boxes and a control series, also consisting of ten settings, were prearranged. Table 1 presents the regular and control settings for each of the several problems, and the total number of doors open in a given series.

TABLE 1

SETTINGS	PROBLEM 1	PROBLEM 2	PROBLEM 3	PROBLEM 4	PROBLEM 5	PROBLEM 6
Doors open (boxes in use) for the ten *regular* settings of problems 1 to 6						
1	1–3	7–9	5–6	2–4	5–7	1–6
2	8–9	1–4	6–8	5–9	5–7	3–9
3	3–7	2–7	1–3	1–7	1–6	4–6
4	7–9	1–6	4–9	7–9	1–6	5–9
5	2–6	4–8	6–8	4–8	4–8	2–7
6	6–8	1–3	2–4	1–9	4–8	4–5
7	5–7	2–5	3–7	1–3	2–5	5–6
8	4–8	1–9	1–2	2–6	2–5	2–8
9	7–9	1–4	2–5	3–9	3–9	3–5
10	1–3	3–8	1–9	6–8	3–9	1–9
Total open for series............	35	50	40	50	50	50
Doors open (boxes in use) for the ten *control* settings of problems 1 to 6						
1	2–4	5–8	5–9	4–8	5–6	5–8
2	6–9	2–6	1–2	1–3	5–6	1–9
3	3–5	1–9	4–8	1–9	4–9	2–5
4	4–9	5–7	1–3	2–6	4–9	5–9
5	6–9	1–4	2–7	6–8	1–5	3–8
6	1–5	4–6	4–5	3–9	1–5	4–7
7	2–8	2–5	1–4	7–9	2–7	5–7
8	3–8	1–3	3–6	1–7	2–7	1–8
9	5–7	1–7	1–3	2–4	3–8	2–5
10	1–9	2–9	1–7	3–7	3–8	3–6
Total open for series............	50	50	41	50	50	51

The chances of correct initial choice in a problem, prior to experience, are presented herewith for the regular and control series of the several problems:

	REGULAR	CONTROL
	per cent	*per cent*
Problem 1	1:3.5 = 28.6	1:5 = 20.0
Problem 2	1:5 = 20.0	1:5 = 20.0
Problem 3	1:4 = 25.0	1:4.1 = 24.4
Problem 4	1:5 = 20.0	1:5 = 20.0
Problem 5	1:5 = 20.0	1:5 = 20.0
Problem 6	1:5 = 20.0	1:5.1 = 19.6

By intent, to render the problems easier, the total number of boxes used in problems 1 and 3 was reduced from 50 to 35 and 40 respectively. All other totals would be either 40 or 50 except for errors in transcription of the original list of settings, which increased by one point the totals for the control series of problems 3 and 6.

SUBJECTS OF EXPERIMENT

Four sexually immature chimpanzees, gifts of the Pasteur Institute of Paris to the Yale Laboratories of Comparative Psychobiology, which shortly after capture in French Guinea were brought to this country in June, 1930, by Professor Henry W. Nissen of the laboratory staff, served as subjects throughout the investigation. In the laboratory records these animals are thus briefly described:

NUMBER	NAME	SEX	HYPOTHETICAL BIRTH-DATE	ESTIMATED AGE AT BEGINNING OF EXPERIMENT
16	Bentia	Female	1926	6 years
12	Soda	Female	1927	5 years
9	Al	Male	1928	4 years
18	Mamo	Female	1928	3 to 4 years

These animals constituted a congenial social group. Much of the time since their arrival in America they have been housed together. Thanks chiefly to the arduous labors of Doctors J.

G. Yoshioka and C. F. Jacobsen in accustoming them to handling and experimental use, they were gentle, tame, and accustomed to collar and leash when I began to use them. At the end of the period of experimentation, September, 1933, Bentia showed indications of approach of sexual maturation; probably menstruation will appear sometime in 1934. Soda, obviously less advanced developmentally, presumably is one to two years younger than Bentia. This is indicated by her behavior as well as by her physical appearance. Al, in mid-childhood, exhibited no signs of sexual maturation. Comparison of him with the others is rendered difficult by reason of sex and age differences. Mamo, decidedly the most juvenile in her behavior and appearance, probably is not less than one year younger than Al. All of the subjects were healthy, vigorous, and ideally available throughout the investigation. Except for our ignorance of birth-date and early life-history, I should not know how to specify primate subjects more suitable for psychobiological studies.

PRELIMINARY TRAINING FOR GENERAL ADAPTATION

The apparatus was constructed in February, 1932. On February 29 preliminary training was begun. As the subjects were not accustomed to handling by me, Doctor Yoshioka, who for a year and a half had been using them in various investigations, facilitated their general adaptation to me and to the new experimental situation by assisting in transferring them to and from the apparatus. For Al and Mamo this was continued about two weeks, and for Bentia and Soda a week longer.

Daily the subjects were taken to the apparatus in pairs, Al with Mamo and Bentia with Soda, for ten to thirty minutes. Initially they were afraid both of O and the apparatus. As soon as they had become accustomed to the situation and to taking food from the cups, effort was begun to induce them to make the circuit promptly from starting point *A*, through one of the boxes whose doors happened to be raised, to alleys *C* and *D* and thence to the starting point. Food was regularly available in the cups. When this adaptation had been achieved, S was required to enter a box whose exit door was closed. All except Soda, with slight aid from O by movement of the appropriate exit door, promptly adapted to this requirement. The progress of Soda was inhibited by timidity until the expedient was tried of raising the box doors only a few centimeters to give her opportunity to manipulate them herself. This she did at once, and within a week she was so far accustomed to passing through the boxes that the entrance doors could be set at standard height.

To prepare them adequately for use in this investigation, Al and Mamo required sixteen days of preliminary experience, and Bentia and Soda seventeen days. This relatively long period of preliminary use was necessary to reduce timidity and to accustom them so thoroughly to apparatus, experimenter, and procedure that they would work freely and naturally. Undoubtedly I could have begun regular experimental use of the animals a fortnight earlier had I not desired excellent general adaptation to the situation, thorough familiarity with it, and confidence in me.

The several subjects may thus be characterized in the light of their behavior during the preliminary training. Mamo was timid, shy, dependent on companions, especially on Al; readily disturbed, emotional, resentful, slow to make the circuit; often and persistently she refused reward of food. Al was aggressive, courageous, emotionally stable, with much initiative; not easily disturbed; he never refused food. Soda was less fearful of O than of the apparatus; always cautious, readily upset emotionally; suspicious of boxes and doors, reluctant to enter a box if its exit door was closed; quick to react, dashing into an open box and through it as if fearful of harm. Bentia, at first distrustful of O, was very cautious in the apparatus and often refused food; usually she was deliberate in selecting a box and in entering and passing through it.

The chronology of preliminary training for general adaptation and of systematic work on problems 1 to 6 is presented by table 2. Experiments were conducted daily from February to July inclusive, 1932, and for the same period in 1933. Work on problem 6 was finally completed in September and October, 1933. Few days were omitted. In general, climatic and other conditions were highly favorable.

TABLE 2

Chronology of multiple-choice work with chimpanzee, 1932–1933

PROBLEM	BENTIA	SODA	AL	MAMO
Preliminary work	Feb. 29–Mar. 22, 1932 (17 days)*	Feb. 29–Mar. 22, 1932 (17 days)	Feb. 29–Mar. 19, 1932 (16 days)	Feb. 29–Mar. 19, 1932 (16 days)
1. Left end	Mar. 24–May 19, 1932 (48 days)	Mar. 24–Apr. 19, 1932 (25 days)	Mar. 21–Apr. 19, 1932 (26 days)	Mar. 21–May 3, 1932 (34 days)
2. Second from right end	May 20–July 19, 1932 (60 days) Feb. 18–Mar. 21, 1933 (25 days)	Apr. 30–July 19, 1932 (80 days) Feb. 18–Mar. 21, 1933 (25 days)	Apr. 30–July 19, 1932 (80 days) Feb. 18–Mar. 19, 1933 (23 days)	May 5–July 1, 1932 (58 days) Feb. 18–Mar. 21, 1933 (25 days)
3. Right end	Mar. 22–Apr. 7, 1933 (17 days)	Mar. 22–Apr. 5, 1933 (15 days)	Mar. 22–Apr. 8, 1933 (18 days)	July 2–13, 1932 (11 days) Mar. 22–Apr. 8, 1933 (18 days)
4. Middle	Apr. 10–May 25, 1933 (40 days)	Apr. 10–May 25, 1933 (40 days)	Apr. 10–May 25, 1933 (40 days)	Apr. 10–May 25, 1933 (40 days)
5. Alternate left and right ends	May 26–July 21, 1933 (56 days)	May 26–July 8, 1933 (44 days)	May 26–July 21, 1933 (56 days)	May 26–July 21, 1933 (56 days)
6. Same box (5)	Sept. 24–Oct. 2, 1933 (9 days)	July 9–21, 1933 (13 days) Sept. 24–29, 1933 (6 days)	Sept. 24–Oct. 1, 1933 (8 days)	Sept. 24–Oct. 2, 1933 (9 days)

Total of regular trials in problems 1 to 6, 10,130; including preliminary, control, and demonstrational, at least 11,000 trials.

* Days of work.

CONDITIONS AND RESULTS FOR PROBLEM 1, LEFT-END BOX

For this problem the following conditions obtained. The first fifty trials were given five per day; thereafter the regular series of ten settings was presented daily, with the exception that on April 17 Bentia and Mamo were given a second series together in the afternoon. Entrance doors to boxes in use were regularly set at height of 70 cm. On completion of a trial all doors in the apparatus were lowered, and the doors were raised for the next setting after S had been returned to *A* (with companion S waiting in *E*).

Food was uniformly used as reward for completion of trial, whether or not by initially correct choice. Incorrect responses, as described below, were penalized by closing of door and confinement in box. Prior to release of S for a given trial a small piece of food was placed at *R*.[2] Orange, grapefruit, and banana were used and the quantity for a trial consisted of $\frac{1}{4}$ small orange or $\frac{1}{3}$ small banana or $\frac{1}{12}$ small grapefruit. This reward was visible to S from compartments *E* and *B* and usually it was noticed prior to response.

In trials 1 to 50 mistakes entailed no other penalty than delay in obtaining reward. No open entrance door was closed until S entered the correct box; its entrance door thereupon was lowered and its exit door immediately raised. Beginning with trial 51, as soon as S entered a box its entrance door was closed. If the box were incorrect, S was permitted to raise the door and retrace its steps to *B*, or in case it did not promptly do so O raised the door. To avoid discouraging S this form of punishment was used irregularly and with extreme caution for a few days. It was made regular procedure for Al and Mamo from trial 81, for Soda from trial 131, and for Bentia from trial 141. In each case the emotional status and degree of adaptation of S determined the procedure. Individual differences were extreme.

Following solution of problem 1 by Al and Soda, punishment of incorrect choices by Bentia and Mamo was increased, on the assumption that adaptation to the problematic situation might thus be facilitated. In case of Bentia, beginning with trial 201 the entrance door to each incorrect box entered was lowered, locked, and S was confined in the box for 10 seconds; with trial 281, confinement was increased to 30 seconds, and with trial 351 to 60 seconds. For Mamo the period of confinement was 10 seconds from trial 231 to solution of the problem.

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[2] Following the period of preliminary work, it was decided to present the reward of food at *R*, in alley *D* of the apparatus, instead of in the food cups. This was done to economize time.

Throughout their work on this problem the subjects were used in pairs to facilitate adaptation and to economize time. At the beginning of the day's work one S was placed in *E*, the other in *A*. They never were together in the same compartment of the apparatus during a series of trials, but they could see one another much of the time. Imitative influence obviously was possible, and the conditions were arranged in part to discover whether the S which from *E* observed the correct response of its companion would thus discover which box to enter and be aided in solving the problem. The subjects served in alternate series from day to day as leader. After the first few weeks of work companionship was unnecessary for reasonably satisfactory conduct of the experiment except in the case of Mamo, who refused to work when alone. For the others, isolation probably would have been more favorable to problem solution, because companionship frequently tended to distract them.

TABLE 3

Influence of leadership in multiple-choice experiment

Results for 180 trials in problem 1 (90 trials leading and 90 trials following)

SUBJECT	SOCIAL STATUS	ERRORS PER SERIES	TOTAL RESPONSES PER SERIES	AVERAGE TIME PER TRIAL	AVERAGE TIME PER TRIAL OMITTING TRIALS 1–40
Bentia........	Leading	4.9	23.8	75.2″	41.1″
	Following	5.4	20.2	62.0	43.5
Soda..........	Leading	4.7	16.2	18.2	12.2
	Following	5.0	16.7	12.5	12.8
Al............	Leading	6.8	20.0	27.8	13.5
	Following	6.1	20.1	17.0	15.1
Mamo.........	Leading	5.7	22.0	34.2	12.4
	Following	5.4	20.6	38.6	11.4

Although evidence of social influence was varied and abundant, there is no adequate proof that any one of the subjects solved the problem imitatively, or indeed was materially aided. Response was facilitated but not definitely directed. The data of table 3, covering the average number of initial errors per series, the total responses (correct and incorrect choices) for series, and time per trial, for each of the four subjects when leading and when following, substantiates the above conclusion.

Presentation of the raw data for the 10,000 multiple-choice trials which are herein reported would require much space. I therefore offer in table 4, as example of the detailed records of response which are available, the data for Al in problem 1, and thereafter, in place of the detailed records, such statistical data as appear to be especially significant.

Since much valuable information is available only in the detailed records of response and in the observer's supplementary notes, they will be filed by the experimenter for consultation by any qualified investigator who may be interested in using them.

Referring to table 4, attention is invited especially to the fact that the control series was twice presented to Al on successive days following his achievement of a perfect series in trials 181 to 190.

As aids to the discovery of the characteristics, relations, and significance of chimpanzee behavior in this experiment, and especially to facilitate conciseness and adequacy of description, the following statistical data have been determined and tabulated for each subject and for all problems which were solved by a given subject. For unsolved problems the method of analysis was applied so far as feasible.

List of statistical and analytical data with brief definitions. 1. Number of incorrect first responses per series of ten trials. 2. Total number of responses per series of ten trials. 3. Number of trials per "setting" prior to solution of *setting* (i.e., disappearance of errors for setting). 4. Total number of responses per "setting" prior to solution of setting (as above). 5. Number of correct first responses for each setting to and including first perfect series. 6. Number of correct first responses without interruption for each setting to and including first perfect series.

TABLE 4

Detailed record of responses (correct and incorrect) of subject Al for problem 1, first box at left end of group

NUMBER OF TRIALS	S.1	S.2	S.3	S.4	S.5	S.6	S.7	S.8	S.9	S.10	RESPONSES	ERRORS	AVERAGE TIME
	1.2.3	**8.9**	**3.4.5.6.7**	**7.8.9**	**2.3.4.5.6**	**6.7.8**	**5.6.7**	**4.5.6.7.8**	**7.8.9**	**1.2.3**			
1–10	3.3.2.3.1	9.8	7.7.3	9.7	6.5.6.2	7.8.8.6	7.7.6.5	7.4	7	3.1	29	9	143.6″
11–20	3.1	8	4.6.7.3	8.9.8.9.7	2	7.6	5	6.8.4	7	3.3.1	23	6	25.0
21–30	3.1	8	6.7.3	7	5.6.2	6	7.5	7.8.4	9.7	3.1	20	7	11.5
31–40	3.3.3.1	9.9.8	7.3	9.7	6.2	8.6	7.5	8.4	7	3.1	22	9	22.6
41–50	3.2.1	9.8	7.3	9.7	4.2	8.6	7.5	8.4	7	3.1	20	9	13.1
51–60	1	9.8	3	8.7	4.6.6.3.6.2	8.6	7.5	8.4	9.7	1	21	7	25.6
61–70	2.1	9.8	5.3	9.7	4.2	8.6	7.5	8.4	7	1	18	8	14.6
71–80	1	9.8	7.4.7.3	9.7	4.6.2	7.8.6	5	4	9.9.7	1	21	6	18.7
81–90	1	9.9.8	7.4.7.3	9.7	6.2	8.7.8.6	5	5.4	9.7	1	22	7	17.7
91–100	1	9.8	5.7.3	9.7	3.6.3.6.2	8.6	7.5	8.8.4	9.7	1	23	8	14.0
101–110	1	9.8	7.5.7.4.7.3	9.7	5.6.4.2	8.6	7.5	7.4	9.7	1	24	8	15.1
111–120	1	8	7.3	9.7	2	8.6	7.5	8.5.8.5.7.4	9.7	1	20	6	13.1
121–130	1	9.8	3	9.7	2	8.6	5	8.6.8.5.4	9.7	1	18	5	12.0
131–140	1	9.8	3	8.7	3.6.2	6	7.5	7.5.7.8.6.4	9.7	1	21	6	11.8
141–150	1	9.8	7.5.3	9.7	2	6	7.5	5.4	7	1	16	5	12.4
151–160	1	9.8	7.4.7.3	9.7	2	6	5	8.5.4	8.7	1	18	5	14.5
161–170	1	9.8	3	8.7	2	6	5	6.4	7	1	13	3	9.8
171–180	1	9.8	3	8.7	2	6	5	4	7	1	12	2	8.1
181–190	1	8	3	7	2	6	5	4	7	1	10	0	5.5
Control........	**2**.3.4	**6**.7.8.9	**3**.4.5	**4**.5.6.7.8.9	**6**.7.8.9	**1**.2.3.4.5	**2**.3.4.5.6.7.8	**3**.4.5.6.7.8	**5**.6.7	**1**.2.3.4.5.6.7.8.9			
	2	6	3	4	6	1	2	3	5	1	10	0	5.5
	2	6	3	4	6	1	2	3	5	1	10	0	5.3

7. Order of increasing difficulty of "settings" as determined from data of 3 to 5. 8. Average number of incorrect responses per box for all settings. 9. Order of increasing difficulty of boxes for the ten settings combined. 10. Average time of trial per series.

As an index of behavioral adaptation and of problem solution, the nature of the initial response to a setting is of conspicuous interest and value. The total number of responses per trial or series is of entirely subordinate importance. For the several subjects of problem 1, these two sets of statistical values have been assembled in table 5.

Especially worthy of comment is the fact that every one of the subjects adapted perfectly to the control series, thus indicating that response to the problematic situation was not dependent upon adaptation to a definite series of specific situations. When on April 13, subject Al in trials 181 to 190 solved problem 1, O entered the following comment: "Al perfect today. I should not have predicted it. Two or three days ago Mamo seemed much nearer success than he. Yet, she lost the cue and today did much more poorly than formerly." It is noteworthy that in her 15th, 16th, and 17th series Mamo made only one error each, and that, as the records show, was always on the same setting, 7–9. Evidently she very nearly achieved success as a result of 150 trials. Similarly, Bentia just missed success in her 11th series.

In accordance with my previous practice (Yerkes, 1916), I arbitrarily used as criterion of problem solution a perfect series of ten trials in succession. This is a rigorous requirement, since it makes no allowance whatever for carelessness or distractions. The primary reason for demanding a perfect series of responses prior to presentation of a new series of settings as control experiment is that the significance of response to the control settings is thus very greatly enhanced. It has been demonstrated (Yerkes and Coburn, 1915; Yerkes, 1916) that an organic type or individual which is able to solve a given multiple-choice problem may be incapable of immediately responding adaptively to the control series.

TABLE 5

Number of responses and number of initial errors per series of ten trials in problem 1, left-end box

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
1–10	51	8	16	4	29	9	45	8
11–20	34	6	17	3	23	6	55	9
21–30	36	6	18	6	20	7	22	7
31–40	28	7	17	6	22	9	29	6
41–50	15	4	20	8	20	9	25	6
51–60	15	5	18	7	21	7	21	6
61–70	21	5	14	2	18	8	22	7
71–80	19	5	25	8	21	6	22	9
81–90	16	5	16	4	22	7	16	6
91–100	16	5	15	4	23	8	18	8
101–110	16	1	19	7	24	8	18	8
111–120	17	6	14	4	20	6	15	5
121–130	15	4	17	6	18	5	15	5
131–140	19	6	15	5	21	6	14	4
141–150	17	4	17	6	16	5	11	1
151–160	20	6	15	5	18	5	11	1
161–170	27	7	13	2	13	3	11	1
171–180	14	3	10	0	12	2	13	3
181–190	19	6			10	0	14	3
191–200	17	5					14	4
201–210	20	6					14	4
211–220	15	3					14	4
221–230	15	4					15	4
231–240	11	1					16	6
241–250	15	5					14	4
251–260	17	6					13	3
261–270	16	4					11	1
271–280	16	5					12	2
281–290	16	6					11	1
291–300	17	5					10	0
301–310	12	2						
311–320	15	5						
321–330	16	6						
331–340	13	3						
341–350	15	5						
351–360	12	2						
361–370	13	3						
371–380	15	5						
381–390	11	1						
391–400	12	2						
401–410	10	0						
Control...	10	0	10	0	10	0	10	0
Control...			10	0	10	0		

Due probably to the asymmetry of the Florida apparatus with respect to return alley (right side only) and to presentation of reward at *R* (right side only), all of the subjects except Soda exhibited from the first in problem 1 strong preference for boxes to the right of the middle of the apparatus, and especially for boxes 8 and 9. This is neither surprising nor undesirable, although quite possibly it somewhat delayed solution of the problem. The relative difficulty of the several boxes, as indicated by the frequency of incorrect responses, is exhibited in table 6 for each individual and for the group. The order of increasing difficulty is presented likewise for the individual and the group. It is worthy of note that this order is almost identical with the box numbering 1 to 9. Needless to say errors were impossible in box 1, as when used it was necessarily the correct box.

TABLE 6

Relative difficulty of boxes (1–9) in problem 1

SUBJECTS	BOXES								
	1	2	3	4	5	6	7	8	9
Average number of incorrect responses per box for all settings									
Bentia	.000	.061	.114	.110	.160	.195	.336	.500	.878
Soda	.000	.139	.315	.084	.167	.222	.333	.444	.185
Al	.000	.079	.334	.263	.246	.263	.527	.447	.719
Mamo	.000	.250	.200	.217	.156	.242	.409	.400	.611
Average	.000	.132	.241	.169	.182	.231	.401	.448	.598
Order of increasing difficulty of boxes (by number) for the ten settings combined									
Bentia	0	2	4	3	5	6	7	8	9
Soda	0	4	2	5	9	6	3	7	8
Al	0	2	5	4 =	6	3	8	7	9
Mamo	0	5	3	4	6	2	8	7	9
Combined order	0	2 =	4	5	3	6	7 =	8	9

Of importance also for the evaluation of various features of response is the relative difficulty of the several regular settings. Pertinent values have been assembled in table 7. Again, data

TABLE 7

Relative difficulty of settings in problem 1

SUBJECTS	SETTINGS									
	1 1–3	2 8–9	3 3–7	4 7–9	5 2–6	6 6–8	7 5–7	8 4–8	9 7–9	10 1–3
Number of trials per setting prior to disappearance of errors										
Bentia	8	40	33	40	17	38	38	34	38	6
Soda	14	15	17	16	11	16	16	16	17	7
Al	7	18	16	18	14	13	15	17	16	5
Mamo	26	24	26	24	25	27	28	25	29	11
Average	13.8	24.3	23.0	24.5	16.8	23.5	24.3	23.0	25.0	7.3
Total number of responses per setting prior to disappearance of errors										
Bentia	19	76	61	92	55	75	62	82	84	10
Soda	25	17	32	25	26	29	26	30	37	14
Al	19	35	45	38	39	30	28	48	27	11
Mamo	48	39	59	55	46	57	46	55	62	19
Average	27.8	41.8	49.3	52.5	41.5	47.8	40.5	53.8	52.5	13.5
Number of correct first responses per setting to and including first perfect series										
Bentia	38	10	24	8	31	15	29	20	15	37
Soda	12	16	7	9	9	7	8	7	5	13
Al	13	4	6	2	8	7	8	3	9	14
Mamo	18	22	16	13	18	14	18	17	4	24
Average	20.3	13.0	13.3	8.0	16.5	10.8	15.8	11.8	8.3	22.0
Order of increasing difficulty of settings (by number) as derived from above data										
Bentia	10	1	5	3	7	6 =	8	9	2	4
Soda	10	2	1	5	4	7	6	8	3	9
Al	10	1	9	7	6	5	3	2	4	8
Mamo	10	2	5	1	7	8	4	3	6	9
Combined order	10	1	5	7	2	6	3	8	4 =	9
Number of correct first responses per setting without interruption to and including first perfect series										
Bentia	33	1	8	1	24	3	3	7	3	35
Soda	4	3	1	2	7	2	2	2	1	11
Al	12	1	3	1	5	6	4	2	3	14
Mamo	4	6	4	6	5	3	2	5	1	19
Average	13.3	2.8	4.0	2.5	10.3	3.5	2.8	4.0	2.0	19.8

are presented for individual and for group. Conspicuous differences in difficulty appear. It is of interest to inquire how these are related to the number of boxes in the group and to the representation of a setting, as in the case of 1–3, which appears as setting 1 and again as setting 10; or for 7–9, used in settings 4 and 9.

The relative difficulty of size-groups is indicated for this problem by the data of table 8. Only three size-groups were used; namely, 2, 3, and 5 mechanisms. It is not indicated that difficulty varies directly with size. Evidently if such tendency exists it is obscured by other influences. There can be no doubt that in case of certain individuals difficulty increases very markedly with increase in the number of mechanisms in use; but in other subjects preferences for particular boxes or prejudices against them completely obscure the influence of size. One might very naturally expect and assume that where a setting is repeated, as in the case of 1 and 10 and 4 and 9 of problem 1, fewer errors

TABLE 8

Relative difficulty of size-groups of box settings for problem 1 as indicated by number of trials and successes

SUBJECTS	NUMBER OF BOXES IN SETTING		
	2 (1 setting)	3 (6 settings)	5 (3 settings)
Number of trials for solution (disappearance of errors)			
Bentia	40.0	28.0	28.0
Soda	15.0	14.3	14.7
Al	18.0	12.3	15.7
Mamo	24.0	24.2	25.3
Average	24.3	19.7	20.9
Number of correct first responses per setting to and including first perfect series			
Bentia	10.0	23.7	25.0
Soda	16.0	9.0	7.7
Al	4.0	8.8	5.7
Mamo	22.0	15.2	17.0
Average	13.0	14.2	13.9

would be made in the second presentation within a series. This expectation is checked and in a measure contradicted by the data of table 9, which presents four measures of the value of repetition. Probably in this instance the individual data are more significant than those for the group. It is indeed surprising that a setting has so little advantage on re-presentation. The fact is highly significant as indicating the relatively slight value for chimpanzee subjects, in solving relational problems, of the characteristics of the particular setting as contrasted with the relationship of the correct mechanism.

TABLE 9

Results for repeated settings in problem 1

DATA	SUBJECT	SETTINGS			
		S.1 1.2.3	S.10 1.2.3	S.4 7.8.9	S.9 7.8.9
Number of trials prior to solution of *setting* (disappearance of errors)	Bentia	8	6	40	38
	Soda	14	7	16	17
	Al	7	5	18	16
	Mamo	26	11	24	29
	Average	13.8	7.3	24.5	25.0
Total responses prior to solution of *setting*	Bentia	19	10	92	84
	Soda	25	14	25	37
	Al	19	11	38	27
	Mamo	48	19	55	62
	Average	27.8	13.5	52.5	52.5
Number of correct trials (to and including perfect series) to solution of *problem*	Bentia	38	37	8	15
	Soda	12	13	9	5
	Al	13	14	2	9
	Mamo	18	24	13	4
	Average	20.3	22.0	8.0	8.3
Number of correct trials without interruption (including perfect series) to solution of *problem*	Bentia	33	35	1	3
	Soda	4	11	2	1
	Al	12	14	1	3
	Mamo	4	19	6	1
	Average	13.3	19.8	2.5	2.0

The daily series of trials usually required for each individual from fifteen to thirty minutes. As examples the following are cited from the average time per trial table prepared for problem 1:

TRIALS	BENTIA	SODA	AL	MAMO
1–10	288.5″	13.7″	143.6″	247.6″
91–100	54.4″	10.7″	14.0″	12.6″
First perfect series	6.3″	5.3″	5.5″	8.7″

It is by no means indicated that the nature or order of difficulty of specific mechanisms, groups of mechanisms, size or repetition of groups determined either the fact or the measure of a subject's success in solving this relational problem. The nature of the solutional process may more profitably be discussed later. Meanwhile, the salient characteristics of the four subjects, as brought to light by work in problem 1, merit description, for they indicate a high degree of individualization and its importance in the study of chimpanzee behavior.

Bentia, persistently distrustful of O and somewhat less so of the apparatus, adapted very gradually to problem 1. Quite commonly she delayed in making the circuit through the apparatus, and almost as commonly she refused to take her reward in spite of obvious hunger and evident desire for it. In the early stages of the experiments she waited for O to operate the box doors instead of doing so herself or attempting to assist him. Whereas occasionally she seemed to be influenced by Soda when following her in a trial, she almost certainly was not aided by imitation in solving the problem, for she made about ten per cent more errors when following than when leading. The experimenter had far greater difficulty in winning the confidence of Bentia than of any of the others. Ultimately this was achieved, but only after months of work.

Soda came to trust the observer almost completely much more promptly than did Bentia; but, on the other hand, she was slower to lose distrust of the apparatus. In speed of general adaptation she far outdistanced Bentia. When working in the apparatus she was much the more nervous and readily upset by novel conditions or distractions, such for example as extraneous noises, heavy clouds, rain, high winds. Although adept in raising entrance and exit doors for passage through the boxes, she was not observed to close any entrance door after an incorrect choice as Al did. Like Bentia, Soda made more errors when following than when leading. Socially she appeared reasonably independent, but quite obviously she relied far more on the experimenter and more persistently tried to get cues from him in responding to the problematic situation than did Bentia.

Throughout the experiment Al appeared far more venturesome and self-reliant than any of his female companions. That this may be attributed primarily to sex is probable, although it must be granted that individuality may be contributory. More quickly by far than the others he achieved excellent general adaptation to observer and apparatus, and subsequently to the procedure of experimentation in problem 1. He alone exhibited repeatedly the highly significant anticipatory act of closing the entrance door of an incorrect box, as if to say: "I have chosen; let me through to food." He did not persist long in this futile gesture of appeal for release, since O raised the exit door only in case of choice of the correct box. For the greater part of the period of work in problem 1, Al seemed the most alert and adaptive of the subjects. His general attitude was one of eagerness and optimism.

Even on completion of work in problem 1, Mamo was markedly dependent socially. It was quite out of the question to use her alone, whereas any one of the others worked with reasonable satisfactoriness in isolation. She expressed her social discomfort by whining, crying, screaming, temper tantrums in which she vocalized loudly while rolling about on the floor of cage, delay in responding or in returning to *A* for another trial, and persistent refusal of food, whatever her degree of hunger. She alone was highly infantile in her behavior toward experimenter, apparatus, and task.

Evidence of definite and gradually or suddenly adopted methods of responding to the multiple-choice situation, or of the trial of hypotheses as Krechevsky has chosen to express it, may be discovered only by analytical study of the detailed records of response, which for condensation are omitted from this report. Attempt will be made to present briefly the pertinent facts for problem 1.

Bentia exhibited the following reactive tendencies. Initially tendency appeared to choose doors to right of middle of apparatus; she made many more erroneous choices to the right of box 5 than to the left. Perseveration was frequent early in the experiment. Not until after 150 trials did she work promptly, steadily, accept reward uniformly and punishment calmly. In the 18th series tendency appeared to run toward the food receptacle and look at the waiting reward before making response. In certain series marked refractoriness and emotional disturbance were exhibited. As a rule, throughout the experiment end boxes were chosen much more frequently than intermediates. In the 34th series, all mistakes (three) were made on box 8, and in the 40th series all (two) on box 9. Definite systematizations of behavior which persisted from day to day are not discoverable, and it must be inferred that they either did not appear or were so transient or obscured by emotional disturbances that they cannot be identified.

Soda, from the point of view of methods of response, seemed more individualistic than Bentia, for she exhibited many mannerisms, most of which were transient and difficult to relate to the task on which she was engaged. Sometimes they seemed playful or diverting, and again like attempts to escape the baffling requirement of the problem. She exhibited initially marked preference for boxes to the right of the middle of the apparatus. This tendency was much less strong than in Bentia. Habitually she made her choices quickly, unless suffering marked inhibition, and dashed through a box as if mistrusting it. There was marked absence of perseveration. In setting 2 (8–9), no errors occurred until the 14th series, when in two successive series, trials 132 and 142, she chose box 9. Why, one must ask, this appearance of error where previously the response had been consistently correct? One may suspect that she was testing the assumption that the right-end box instead of the left-end might prove satisfactory. For her, setting 1–3 proved relatively easy, whereas setting 7–9 was relatively difficult. Possibly this is because of a strong bias in favor of right-end boxes, and the peculiar attraction, perhaps because of location of food at the right, of boxes 8 and 9 when used in combination with 7. Solution of the problem finally came rather abruptly, and the control series did not in the least disturb or upset her. Systematizations of response are conspicuous by their absence.

In the case of Al, aside from marked preferences for end boxes, methods of response are not observable. Confusion or excitement appeared relatively rarely, and seldom was more than a single error made in a given trial. Solution was decisive and the control series was responded to perfectly without disturbance.

Mamo, as companion of Al, contrasts interestingly with him. Perseveration of response was conspicuous in her early trials, as was also strong preference for boxes to the right of the middle of the apparatus. Far more often than the other subjects, Mamo chose intermediate instead of end boxes. Finally, however, her mistakes were reduced practically to right-end choices. Systematizations of response are not evident. Peculiarly interesting and significant is the reappearance of errors in a setting following many successes. This may be supposed to indicate change in method of response, confusion because of some distracting circumstance, or loss of a cue on which the animal had come to depend.

As to modes of solution of problem 1, it suffices to direct attention to the statistical data already presented and to the composite curve of error presented as figure 4. The data for this plotting are found in table 5 (p. 18). Neither the array of errors in daily series, with its gradual diminution to zero, nor the composite curve of problem solution, suggests the occurrence of sudden or abrupt solution as contrasted with gradual approximation to adequacy of response. But if sudden solution is slightly indicated, so also is adaptation to specific settings and achievement of solution by accumulation of correct responses to the stated and regular series of such specific settings. From the results of problem 1, it is impossible to infer with certainty either that the subjects discovered the spatial relationship which we designate as left-endedness, or that they became so proficient in responding to specific situations in which left-endedness appeared that despite change of settings, as well as of the order of their appearance, they were able to adapt perfectly. It is my opinion that the evidence favors solution by response to relationship, and that only on that basis can the success of the subjects in responding promptly, with assurance, and correctly to the series of control settings be adequately explained.

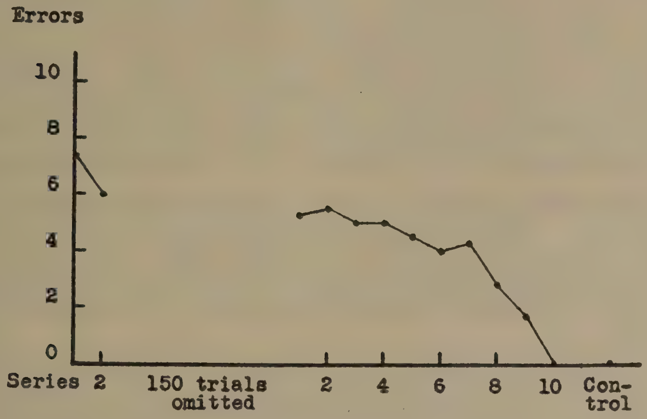

FIG. 4. COMPOSITE ERROR CURVE FOR FOUR SUBJECTS IN PROBLEM 1, LEFT-END BOX

The average number of incorrect trials for the first two series and the last ten series is used to exhibit the course of problem solution. No errors were made in the control series.

CONDITIONS AND RESULTS FOR PROBLEM 2, THE BOX SECOND FROM THE RIGHT END

Although problem 2 presumably is more difficult than problem 1, it was thought that because of their perfected general adaptation and their experience in problem 1 the subjects would succeed promptly in solving the second problem. The opposite proved to be true, and in the course of months of work Mamo alone succeeded in meeting the criterion of success; and even in her case, adaptation to the control tests was imperfect.

After completion of problem 1, and with interims of from one day to approximately two weeks, as appears from table 2 (p. 12), without attempt to eradicate experimentally the various reactive tendencies which had been acquired, problem 2 was presented. Initially, as for problem 1, the subjects were used in pairs, but with the exception of a few series, the possibility of success by following the leader was eliminated by having the first animal work two trials in advance of the second. Subsequently the subjects were used alone in the experiment, Bentia beginning with trial 201, Soda and Al with 351, and Mamo with 321.

With the exception of Bentia, who throughout work on the problem was given either ten or twenty trials per day, the subjects started with five trials per day, after ten days were increased to ten, and subsequently to twenty. No indications appeared of special advantage in fewer or more than the regular series of ten trials per day. When two series were given, they always were separated by at least an hour, and the same total quantity of food was provided as reward as in the case of the single series of ten settings.

At the beginning of work on problem 2, in order to avoid discouragement in making the transition from the requirements of the previous problem to the new one, the subject, after five minutes of futile effort to locate the correct box, was aided by the experimenter. Usually it sufficed to unlock the exit door of the correct box; occasionally it was necessary to raise that door slightly or to attract attention to it by rattling it. It was later found more satisfactory to aid the subject after five incorrect responses than after a given time interval. At first, punishment for mistakes was omitted; subsequently it was introduced cautiously and according to the degree of adaptation and temperament of the subject. It was introduced as early as trial 51 (Bentia), and as late as trial 101 for the other subjects. Early it became clear that to follow a uniform procedure arbitrarily with all subjects would lessen rather than otherwise the degree of comparability of results, and either seriously delay or entirely prevent the adaptation of an individual.

As previously, bits of food were supplied at *R* as rewards. In the course of the experiment both rewards and punishments were varied experimentally as will presently be indicated. At the outset, both varieties of motivational condition were arranged in the light of the results of problem 1. It appeared desirable to stir the subject's interest and desire to complete the circuit of the apparatus successfully by offering a lure, and within limits to discourage careless responses by such penalty as the closing of wrong entrance doors, or in addition to that, the confinement of an animal in wrong boxes from five seconds to sixty seconds.

The special motivational conditions whose value was tested in connection with problem 2 may more appropriately be described after consideration of the outcome of the first few weeks of work by the several subjects, and especially of the success of Mamo.

As previously, response and error data are presented for all subjects. It is apparent from these data, as arranged in table 10, that in the first 400 trials no one of the subjects except Mamo made such consistent improvement as to justify one in predicting solution of the problem. Mamo, however, in her 17th series, made no mistakes. Her success came without warning and following 160 trials in which her best daily record was 70 per cent correct choices.

The following facts taken from the observer's notes on the experiment are of peculiar interest and importance:

> May 24, the date of the 17th series, was climatically perfect. About Al's behavior there was nothing unusual to remark, but when I went into their quarters to take Al and Mamo to the experiment she came to me eagerly as if anxious to get to the apparatus. This, I think, never had happened before. She seemed so glad to see me and eager for work that I was much surprised and therefore made special note of the fact. Al, it is recorded, was his usual independent and playful self. Mamo made a perfect score without evidence of difficulty. I was amazed each time she chose correctly and took special pains to avoid the possibility of cues from the observer and from his manner of manipulating the apparatus. Her success is especially interesting in the light of her attitude toward me in the quarters. It makes one wonder whether she had a premonition of success and if so whether it was responsible for her unusually favorable attitude toward the experiment.

TABLE 10

Number of responses and number of initial errors per series of ten trials in problem 2 (1932), box second from the right end

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
1–10	48	9	71	10	106	10	64	10
11–20	93	10	67	9	86	10	64	10
21–30	62	8	68	8	185	10	64	7
31–40	47	9	66	9	159	7	32	6
41–50	23	6	79	9	109	10	29	7
51–60	33	7	40	6	44	8	22	6
61–70	24	5	56	7	65	8	29	7
71–80	27	6	38	5	42	10	24	7
81–90	26	6	38	6	27	9	34	8
91–100	30	4	72	8	26	9	26	3
101–110	27	8	23	5	50	9	36	9
111–120	62	6	37	5	62	10	33	7
121–130	25	4	23	6	36	10	31	5
131–140	24	6	28	8	33	10	32	6
141–150	20	5	17	3	40	10	31	5
151–160	16	3	26	5	42	10	25	5
161–170	17	5	26	4	32	9	10	0
Control...							29	6
171–180	31	6	35	7	29	10	28	5
181–190	28	7	20	6	28	9	38	9
191–200	18	7	19	6	27	8	31	8
201–210	23	5	29	6	32	8	27	8
211–220	26	7	22	5	27	9	19	5
221–230	24	6	19	6	66	7	19	5
231–240	21	7	32	7	42	8	14	3
241–250	23	4	26	4	18	6	18	6
251–260	31	6	16	4	28	7	18	5
261–270	25	7	15	5	20	6	22	3
271–280	28	8	14	4	18	8	13	3
281–290	31	7	19	5	22	8	25	2
291–300	21	7	15	3	20	8	59	5
301–310	23	5	19	5	15	5	22	8
311–320	19	4	13	3	18	6	27	8
321–330	23	7	15	4	37	9	18	3
331–340	21	6	25	8	28	8	18	4
341–350	26	5	19	5	20	5	26	5
351–360	17	3	25	5	36	9	20	3
361–370	18	5	27	7	51	9	13	2
371–380	19	3	29	6	37	7	13	3
381–390	22	4	24	6	32	7	26	4
391–400	31	8	41	7	42	8	33	5
401–410	10*	4	28	6	29	7	22	6
411–420	10*	4	15	3	21	6	18	3
421–430	10*	8	16	3	31	8	24	4
431–440	10*	8	23	5	23	6	22	5
441–450	10*	6	28	5	27	7	16	6
451–460	10*	4	18	5	28	10	16	4
461–470	10*	5	18	5	21	8	14	2

TABLE 10—*Concluded*

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
471–480	10*	4	21	8	27	9	12	2
481–490	10*	4	29	9	60	9	12	2
491–500	10*	4	39	6	54	7	12	2
501–510	18	6	32	5	43	8	15	2
511–520	15	3	33	7	26	5	10*	2
521–530	18	6	44	8	28	6	10*	3
531–540	40	7	50	9	22	5	10	0
541–550	21	6	25	8	19	5	10	0
Control...							10	2
Control...							10	2
551–560	26	5	10*	5	10*	7		
561–570	26	7	10*	5	10*	3		
571–580	19	7	10*	7	10*	5		
581–590	16	6	10*	4	10*	4		
591–600	16	6	10*	3	10*	9		
601–610	26	7	10*	2	10*	5		
611–620	16	6	10*	5	10*	5		
621–630	18	7	10*	3	10*	7		
631–640	22	7	10*	2	10*	5		
641–650	17	6	10*	6	10*	5		
651–660	24	7	26	5	20	8		
661–670	17	7	33	8	19	5		
671–680	30	5	46	8	16	4		
681–690	37	5	26	7	15	5		
691–700	33	6	19	4	14	4		
701–710	12	2	15	3	15	5		
711–720	18	2	30	8	12	2		
721–730	16	4	32	8	15	3		
731–740	14	3	23	7	12	2		
741–750	14	3	17	7	12	2		
751–760			21	6	18	6		
761–770			19	7	15	5		
771–780			23	7	17	7		
781–790			13	3	14	4		
791–800			19	4	16	6		
801–810			18	6	23	3		
811–820			26	7	19	4		
821–830			18	5	23	7		
831–840			19	5	23	2		
841–850			15	3	23	5		
851–860			16	2	16	1		
861–870			17	4	18	3		
871–880			14	2	12	1		

* Only one choice permitted.

On the day following her solution of problem 2, the control settings were presented to Mamo. By inexcusable oversight or confusion on the part of the observer, the procedure was changed from that previously used in that the subject, instead of being permitted to pass through the first box entered whether or not it were the correct box (see page 7), was required to make choices until it entered the correct box and then allowed to pass through and take its reward. The latter procedure evidently is much more likely to disturb the animal than the former. As it happened, Mamo made six errors in this series. She was quite obviously irritated by her failures and confused. In all probability she would have made some errors, but fewer, had the standard procedure been employed.

Because of her failure to meet the requirements of the control test it was decided to continue Mamo in the experiment by presenting the regular series. Oddly enough, the results from trial 171 on suggest that she had completely lost her cue or cues, and despite her success in the 17th series was unable to do better than she had immediately prior to it. These facts are inexplicable on the assumption that the subject responded to specific settings. Instead, it seems probable that attention was focused, during the 17th series, on the relation of the correct box to the group, secondness from right end, but that the animal's grasp of this relationship was insecure and consequently the radical change in the situation which resulted when the control settings were presented completely destroyed the incipient adaptation and caused Mamo to revert to her previous mode or modes of response, and also to her previous attitude toward the requirements of the experiment.

Between the 18th series of responses and the 53d, Mamo's scores never exceeded 80 per cent correct. Beginning with trial 511, the procedure of experimentation was radically changed with respect to motivational factors. The subject, instead of being permitted to respond until it discovered the correct box, was allowed to pass through the first box chosen in each trial and was rewarded only in the event of a correct choice. This of course means, as the tabulated results show, limitation of total responses per series to ten. Following this change Mamo was greatly stirred and quite clearly made maximal effort to respond correctly. In the first series, the 52d, she made two mistakes;

in the second, the 53d, three mistakes. But on the following day, in the 54th and 55th series, she responded with perfect adaptation.

On the next day, as test of relational character of response, the control series was presented in accordance with usual procedure, that is, by allowing the animal to pass through the first box chosen and thereupon rewarding it. The series was presented twice, with an interval of one hour between, and in each instance two errors were made. It is clear therefore that, even after 550 trials in problem 2, Mamo was incapable of responding to the relation of secondness from the right end when the settings and their order of appearance were altered. In other words, she seemed incapable of definite generalization of response, and to the observer it appeared as though her grasp of the necessary cue to correct response was very insecure and that she was capable of satisfactory adaptation only under highly favorable external and internal conditions.

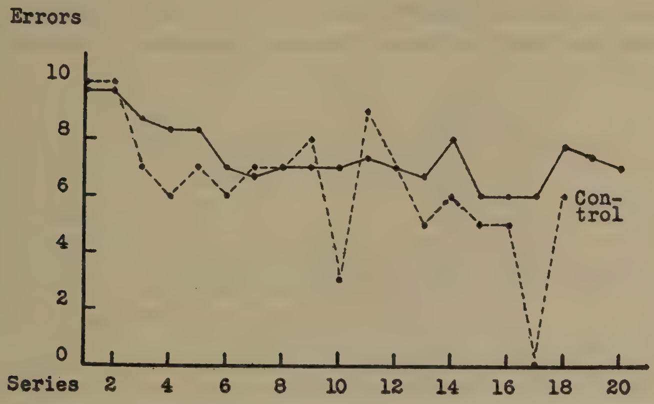

FIG. 5. ERROR CURVE FOR PROBLEM 2, SECOND BOX FROM THE RIGHT END OF GROUP

The dotted line represents the results for Mamo. In a "control test," following her first perfect series, she made six errors. The solid line indicates the average errors per series for Bentia, Soda, and Al, all of whom failed to achieve solution, in their first twenty series.

Figure 5 visualizes the course of initial success by Mamo and, by contrast, the failure of the other subjects (combined) to approach solution on the basis of two hundred trials. The abruptness of Mamo's success is noteworthy.

Other significant statistical data for the responses of Mamo in problem 2 are presented in tables 11–14. These are based upon her solution of the problem, secondarily, after 540 trials.[3]

The relative difficulty of the several response mechanisms and their order of increasing difficulty are markedly different for Mamo in problem 2 and problem 1 (cf. tables 11 and 6, p. 19). Whereas in the earlier problem, boxes to the right of the middle of the apparatus were very greatly preferred, in problem 2 such preference, although appearing, was relatively slight, and errors on boxes 4 to 8 were far more frequent than on 1, 2, 3, and 9.

TABLE 11

Relative difficulty of boxes (1–9) in problem 2

SUBJECT	BOXES								
	1	2	3	4	5	6	7	8	9
Average number of incorrect responses per box for all settings									
Mamo.............	.219	.366	.372	.420	.458	.462	.468	.452	.298
Order of increasing difficulty of boxes (by number) for the ten settings combined									
Mamo.............	1	9	2	3	4	8	5	6	7

For the several settings of problem 2, difference in difficulty is by no means so pronounced as might have been expected. Responses naturally tend to be proportional to the number of boxes in use, but analysis by size of group yields results, table 13, which show that difficulty is not dependent primarily upon the number of mechanisms in the group. Three mechanisms, it is true, required fewer trials for solution than did any of the larger groups, but, on the other hand, the five and nine mechanism groups each required the same number of trials.

It is particularly interesting to note that the only repeated setting in problem 2, 1–4, used in settings 2 and 9, was difficult

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[3] Trials 511–530 were omitted in the statistical treatment of data.

TABLE 12

Relative difficulty of settings in problem 2

SUBJECT	SETTINGS									
	1 7–9	2 1–4	3 2–7	4 1–6	5 4–8	6 1–3	7 2–5	8 1–9	9 1–4	10 3–8
Number of trials per setting prior to disappearance of errors										
Mamo.......	42	50	50	45	51	47	47	51	45	49
Total number of responses per setting prior to disappearance of errors										
Mamo.......	77	130	146	130	134	86	128	216	98	138
Number of correct first responses per setting to and including first perfect series										
Mamo.......	37	24	20	21	19	36	28	24	31	22
Order of increasing difficulty of settings (by number) as derived from above data										
Mamo.......	1	6 = 9		7	4	2	10	8	3	5
Number of correct first responses per setting without interruption to and including first perfect series										
Mamo.......	10	2	2	7	1	5	5	1	7	3

TABLE 13

Relative difficulty of size-groups of box settings for problem 2 as indicated by number of trials and successes

SUBJECT	NUMBER OF BOXES IN SETTING				
	3 (2 settings)	4 (3 settings)	5 (1 setting)	6 (3 settings)	9 (1 setting)
Number of trials for solution (disappearance of errors)					
Mamo.....................	44.5	47.3	51.0	48.0	51.0
Number of correct first responses per setting to and including first perfect series					
Mamo.....................	36.5	27.7	19.0	21.0	24.0

of solution by Mamo, despite double frequency of presentation, and exhibits almost as many errors, 45 versus 50 (table 14), for the second presentation as for the first. Again it may be remarked that were the subject depending upon the characteristics of specific settings, success on re-presentation should be much more frequent than for first presentation in a given series.

Referring now especially to the responses of Bentia, Soda, and Al in problem 2, it was decided, inasmuch as their daily error records up to the 40th series gave slight indication of progressive improvement, or of approaching solution of the problem, that procedure should be changed in order to test experimentally the value of different motivational factors and combinations thereof. The first radical departure from the procedure used in problem 1 was to permit only one response in each trial and to supply reward only in case of correct response. Beginning for Bentia with trial 401, Soda and Al with trial 551, and Mamo with trial 511, this motivational condition was used either until solution of the problem (by Mamo only) or for 100 trials.

TABLE 14

Results for repeated settings in problem 2

DATA	SUBJECT	SETTINGS	
		S.2 1.2.3.4	S.9 1.2.3.4
Number of trials prior to solution of *setting* (disappearance of errors)	Mamo	50	45
Total responses prior to solution of *setting*	Mamo	130	98
Number of correct trials (to and including perfect series) to solution of *problem*	Mamo	24	31
Number of correct trials without interruption (including perfect series) to solution of *problem*	Mamo	2	7

Persistent failure of the subjects, with the exception of Mamo, to achieve success justified, it seemed, varied and repeated changes in motivational conditions. To describe these in detail for each individual would be tedious; they are summarized herewith under a few categories and without specific reference to individual subjects. In some instances a given condition was used continuously for several days, mostly for either 50 or 100 trials, and again, abrupt changes were made from day to day, to test both continuity of condition and sudden change which might be expected to shift the direction of the subject's attention and perhaps disturb response tendencies which had become almost automatic.

Variations of reward included the following: Regular presentation of desired food as reward following completion of every trial, or as indicated above, the limitation of reward to initially correct responses. The presentation of a relatively large quantity of food for initially correct response and of a relatively small quantity for secondarily correct response. The use of a much desired or preferred food in case of initially correct responses and of a relatively disliked food for secondary successes. Degree of hunger was varied from that resulting from period of twelve to a maximum of approximately twenty-four hours without food.

The number of trials per day was varied, partly for convenience, partly for experimental evaluation, from one-half series (5 trials) to two series (20 trials). The advantage, if any, appeared to be in favor of the regular 10-trial series daily.

Definite punishment for incorrect response included the closing of the entrance door of a wrong box momentarily; closing and locking the door; closing the door and confining the subject in the box for five, ten, thirty, or at most sixty seconds. It was found inexpedient to use long confinement repeatedly, so a common procedure was to use long confinement for the first mistake in a given trial and confinement not exceeding ten seconds for subsequent mistakes. Punishment by confinement for the first mistake only also was tried.

To test the value of an auditory signal as indicator of incorrect response, blast on a police whistle, two to four seconds, immediately following incorrect response, the dropping of the entrance door of an incorrect box so that it banged, and vocal reprimand by O for mistake were employed singly. Seemingly the sound of the whistle was not attributed to O, whereas the banging of the entrance door and vocal reprimand immediately were. The whistle caused relatively slight emotional disturbance after a few applications, whereas the banging of the entrance door and the verbal signal of the experimenter markedly disturbed the subjects and tended to inhibit response. It was not indicated that auditory signal of incorrect response facilitated problem solution.

Among series in which punishment was employed were interspersed some devoid of punishment. This was done with the intention of testing the value of radical change and variety.

It became increasingly evident as work on problem 2 continued that the animals, without respect to appropriateness, tended to use certain patterns of response and to accept the situation as though it were a necessary evil beyond their ability to ameliorate. Although often it appeared that a change in conditions had stirred the interest and optimism of a subject, this with few exceptions proved to be transient, and from the statistical results it is impossible to say that one combination of motivational factors is superior to another. The subjects almost invariably were alert, eager to obtain the reward of food, and to all appearances entirely adequately motivated. They tended, however, after weeks of work on problem 2, to go through a routine instead of seeking new modes of response and resultant solution of the problem.

Partly because of previous experience with other mammals which without particular difficulty had succeeded in solving the problem of the second mechanism from one end, I was extremely loath to discontinue the work of my chimpanzee subjects on this problem. Consequently I went forward with it until the end of the first season, when the necessity of migration from the Florida Station to New Haven compelled temporary discontinuance of the investigation. At that time, Bentia, on the basis of 750 trials, had achieved in two relatively late series 80 per cent of correct choices; Soda, on the basis of 880 trials, had made a similar record, while Al, with 880 trials, had achieved 90 per cent correct in two series. These facts suggest that had it been possible to continue the observations for a week or a month, all of the subjects might have achieved success. On this score I was so optimistic that I could not make up my mind to abandon the problem entirely, although I was fully convinced that the continuance of its use entailed serious disadvantages because of the development of automatisms which would undoubtedly be extremely unfavorable to success in other problems. After weighing the several advantages and disadvantages, I decided to re-present problem 2 at the beginning of my second season of work, 1933, and to attempt thus to discover whether a period of rest might enable Bentia, Soda, and Al to succeed where previously they had failed, and also whether Mamo, on review of the problem, would exhibit perfect adaptation, or lacking that, would promptly re-adapt.

Conditions on resumption of work, February 14, 1933.

Each of the four subjects was given a preliminary test in the apparatus to assure the persistence of satisfactory general adaptation. Four days later regular work was begun. Each animal was used alone. Initially, after five mistakes in a trial O aided the subject in locating the correct box by unlocking the exit door, and if necessary, moving it slightly. The entrance door was closed after the animal only in case of a correct choice. There was no punishment whatever for mistakes. Food was presented at *R* on completion of each trial. The regular series of ten settings was presented daily. The animals were used in order of diminishing age: Bentia, Soda, Al, Mamo.

From the first the general adaptation of each subject was excellent and the experiment proceeded without difficulty or irregularity. The results assembled in table 15 indicate that no one of the subjects solved the problem within the ten days of work (100 trials) provided. Bentia, in her 7th continuation series, made only one error; Soda, in her 3d series, made a single error; Al made not less than four errors in any series, and Mamo, having it would appear completely lost her cue, made from four to ten errors in each series.

It should here be stated, in partial explanation of Mamo's failure to succeed when problem 2 was re-presented to her, that following her solution of the problem in 1932, problem 3, the right-end box, was presented to her and solved. Consequently she had acquired certain tendencies of reaction in the multiple-

TABLE 15

Number of responses and number of initial errors per series of ten trials in problem 2 (1933)

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
1–10	18	5	12	2	26	6	34	6
11–20	25	8	24	4	22	6	26	6
21–30	15	5	15	1	19	4	37	10
31–40	21	4	26	5	21	6	38	10
41–50	22	5	26	6	15	5	39	9
51–60	16	4	13	3	21	6	26	6
61–70	11	1	21	6	18	6	22	4
71–80	15	3	21	6	21	7	28	8
81–90	14	4	17	4	19	6	19	5
91–100	12	2	20	7	17	4	32	7
Stage 1 (1–4)								
1–10	33	9	15	2	13	3	11	1
11–20	15	4	20	7	15	4	11	1
21–30	14	3	13	2	10	0	10	0
31–40	12	2	14	2				
41–50	13	3	12	1				
Stage 2 (4's)								
1–10	13	3	24	5	21	6	13	2
11–20	12	2	13	2	23	6	16	3
21–30	12	1	13	2	22	8	14	4
31–40	12	2	14	2	18	7	11	1
41–50	13	3	28	4	33	6	11	1
51–60	15	4	24	4	28	6	12	1
61–70	17	5	22	5	22	6	10	0
71–80	17	3	20	5	33	6		
81–90	20	5	20	5	27	7		
91–100	19	5	25	5	19	5		
Stage 3								
101–110							11	1
111–120							15	5
121–130							11	1
131–140							13	2
Control...							12	2

choice apparatus, not shared by the other subjects, which were unfavorable to immediate re-adaptation to problem 2. I have no explanation whatever for the persistent failure of the other subjects to solve this problem. Certainly Bentia and Soda barely missed success, and Al, at the end of his work in 1932, quite evidently was on the threshold of perfect adaptation, yet failed to cross it.

Still reluctant to abandon use of the problem, I decided to try the experiment of markedly simplifying its form and of presenting it in stages of increasing complexity and difficulty. Three stages were selected: the first, designated in the tables as stage 1, consisted of the presentation of the setting 1–4 ten times in succession as regular series; the second, stage 2, the presentation of groups of four boxes located at various points in the apparatus, as for example, the settings 4–7, 1–4, 6–9; and the third, stage 3, the regular series of settings originally used in problem 2.

Briefly, it appears from table 15 that in stage 1, the 1–4 setting, Bentia and Soda failed to adapt in 50 trials, whereas Al and Mamo adapted perfectly in 30 trials.

In stage 2, settings describable as 4's, Mamo adapted in 70 trials, whereas no one of the others achieved a perfect series. Bentia's nearest approach was 90 per cent correct in her 3d series; Soda's 80 per cent in her 2d, 3d, and 4th series, and Al's 50 per cent correct in his 10th series.

The regular series of settings was presented to Mamo following her success in stage 2, and in two of four series she made 90 per cent correct choices. Thereupon the control series was presented and she made two errors. From these results it is apparent that Bentia and Soda less closely approached successful adaptation than did Al and Mamo. For the latter especially, solution always seemed to be just around the corner, almost within grasp, but evasive. Was this because the problem is too difficult, and if so, why should such be the case for chimpanzee and not for pig (Yerkes and Coburn, 1915), or monkey (Yerkes, 1916)? Were there perhaps conflicting reactive tendencies which rendered solution extremely difficult or impossible, or is the chimpanzee's mode of attempted solution for some reason relatively unfavorable? Whatever the answer to these questions, Mamo has the distinction of having solved the problem of second mechanism from the right end by some process other than definite grasp of the significant relationship.

Systematizations or methods of response were not numerous, nor were they definitely or persistently followed in this problem. Naturally enough the left-end mechanism, and by contrast the right-end mechanism, tended to be preferred over all others. There appeared also from time to time preference for a particular mechanism, and again, tendency to choose an end mechanism and to progress systematically through the group until the right box was entered.

At this point problem 2 was abandoned for one which presumably would be relatively easy of solution. Because of their months of futile labor on problem 2, the subjects were in relatively unfavorable condition for continuation of the investigation. Despite their perfect general adaptation to the experiment, it would have been entirely unreasonable to present immediately a difficult relational problem.

CONDITIONS AND RESULTS FOR PROBLEM 3, RIGHT-END BOX

Immediately following discontinuance of work on problem 2, the problem definable as right-end mechanism and designated as problem 3 was presented. For dates of presentation, see table 2, p. 12. After Mamo completed her work on problem 2 in July, 1932, she was given problem 3. The other subjects did not begin work on the problem until March, 1933, when it was re-presented to Mamo for review and, if necessary, re-learning.

My expectation and prediction were that problem 3 would prove much easier of solution by my subjects than had problem 1, because of their improved general adaptation to the multiple-choice apparatus and their success in solving problem 1. But reactive tendencies acquired in problems 1 and 2 produced conflicts and inhibitions which undoubtedly retarded the solution of problem 3.

Because of the extreme difficulty which the animals had with problem 2 and the possibility that motivational conditions were not optimal, it was sought, in problem 3, so to modify the combination of motivational factors as to test more thoroughly than previously the value of inhibitors of incorrect choices, as contrasted with reënforcers of correct responses. To this end the apparatus was arranged for use of induced current stimulation. This was effected very simply by attaching to the floor of the several boxes strips of sheet copper $\frac{1}{16}$ inch in thickness by 1 inch in width. Beginning at the front, or entrance door end, of the boxes, twelve such strips were tacked to the floor $1\frac{1}{2}$ inches apart. A Porter inductorium and two dry cells, rated at $1\frac{1}{2}$ volts, supplied induction shocks.

The following conditions of work obtained. It is necessary to describe first the conditions for Mamo in 1932, and thereafter those which apply to the four subjects alike during the season of 1933. Mamo, in 1932, was used alone. Mistakes were not punished in the first 40 trials, and initially she was aided by the experimenter if not successful in a given trial within two minutes. Punishment by closing of entrance door for initial mistake only and confinement for ten seconds was introduced with trial 41. For trials 81–90 punishment was omitted; it was resumed in the following series, and beginning with trial 131 it was coupled with the use of preferred food for initially correct responses and disliked food for trials in which mistakes were made. Except on July 7, when the 9th series of trials was given alone, two series (20 trials) were given daily, separated by one to two hours.

For the other subjects, and also for Mamo in review of problem 3 in 1933, the general conditions were as follows. Only minor variations were made in adaptation to the temperament and condition of the individual subject.

Each subject was used alone throughout problem 3. Reward of food was given at the end of each trial whether or not the initial response was correct. Ten trials, a single series, were given daily. For the first 50 trials there was no penalty for incorrect choices and the entrance door was closed after the animal only for correct responses. Beginning with trial 51, the 6th series, the entrance door was closed momentarily whenever a box was entered. This procedure was discontinued at the beginning of the 9th series with trial 81, when electric stimulation as penalty for an incorrect choice was introduced. Initially it was used only in case of the first mistake for a given trial. The coil was set at 7 for preliminary trials, since under that condition the experimenter received an appreciable and slightly disagreeable stimulus when he tested the electrodes with his fingers. In accordance with the response of the subject, the strength of the electrical stimulus was increased regularly, and eventually the following settings were used: Bentia and Al, coil at 4 on scale; Soda and Mamo, coil at 5.

Attempt was made to hold each subject to maximal attention and effort by providing desired food reward for correct choices and by penalizing incorrect responses by stimulating the subject electrically. The electrical stimulus caused no pronounced disturbance; even when first used it merely surprised the animals and caused them to examine the floor of the boxes. They were interested and evidently somewhat mystified. In no case did they clearly attribute their peculiar experience to the experimenter. Commonly they attempted to avoid the shock when the coil was set at 5 or thereabouts. Soda and Mamo were markedly more responsive to the electrical stimulus than were Bentia and Al. It was not determined whether this was due to difference in sensitiveness or to degree of responsiveness.

In considering the results of this experiment it should be borne in mind that motivational conditions in the 1932 solution of the problem by Mamo were very different from those used for the four subjects the following season, since originally electrical stimulation was not used.

In the statistical data for problem 3 the responses and errors per series exhibit the following noteworthy facts and relations. Bentia, between the 10th and 11th series, improved as indicated by the change from 40 per cent to 90 per cent correct responses. Evidently she just missed success in the 11th series, and despite her failures in two subsequent series hers probably was sudden discovery of the relational cue, although it was not followed immediately by solution of the problem. Actually, the 14th was her first perfect series.

Soda, much upset by the change in the apparatus due to its electrification, refused at the beginning of problem 3 to react freely and promptly as customarily, and in several trials of the first four series she had to be aided by O, to avoid complete discouragement and cessation of effort. Aid was given as necessary by unlocking, and sometimes moving slightly, the exit door of the correct box. Because of this irregular help the records of responses and errors in trials 1–40 for Soda are valueless and do not appear in table 16. Between Soda's 9th and 10th series, successes increased from 50 to 80 per cent, and of all the subjects she solved problem 3 most quickly and with the smallest total of

TABLE 16

Number of responses and number of initial errors per series of ten trials in problem 3, right-end box

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
1–10	25	9	—*	—*	22	6	24	10
11–20	23	8	—*	—*	28	7	24	9
21–30	20	8	—*	—*	25	6	41	9
31–40	22	6	—*	—*	22	5	34	9
41–50	20	8	20	5	22	6	18	7
51–60	22	9	21	4	19	5	21	8
61–70	18	7	16	4	20	6	13	3
71–80	19	8	15	3	16	6	14	4
81–90	18	6	15	5	17	6	13	3
91–100	17	6	12	2	22	6	16	6
101–110	11	1	12	2	22	10	16	4
111–120	12	2	10	0	15	5	18	4
121–130	11	1	10	0	13	3	13	3
131–140	10	0			11	1	12	2
141–150	11	1			11	1	12	2
151–160					11†	1†	10	0
161–170							10	0
Control...	10	0	10	0	10	0	10	0
Control...	11	1	10	0	11	1	10	0

* Electrification—aided.

† Irregular—Al did not make perfect score. Trials 151–160 treated as perfect series.

errors. Quite possibly the aid given her at the beginning of the experiment contributed to her early success. It was not evident that she was more interested, attentive, careful, or worked harder in the experiment than did the other subjects.

Al improved slightly, if at all, to judge by the record of errors, prior to his 13th series in which he was 70 per cent correct. That series, in the opinion of the experimenter, marks his discovery of the essential relationship and his solution of the problem. For thereafter and in three successive series, he made only one incorrect response and that in each case on the same setting, no. 10, boxes 1–9. After this had happened on three successive days, I decided that the error almost certainly was due to some acquired reactive tendency toward box 9 and that quite possibly the substitution of another setting for 10 would demonstrate his ability to meet the criterion of success. To test this assumption rigorously he was given the control series following his 16th regular series, and on the basis of perfect adaptation to the control settings he was rated as having achieved solution of problem 3. Consequently, for statistical purposes, his 16th series, trials 151–160, is considered correct and indicative of problem solution.

This case, in which a certain type of error persisted in series after series because of selection of a particular reaction mechanism, is not unique. In most of the problems at one time or another, and more or less frequently for each subject, precisely this type of reactive tendency manifested itself. Occasionally no doubt it delayed success, and sometimes, as in this instance, it undoubtedly obscured problem solution.

Gradually, in the course of 150 trials, Mamo approximated adequacy of response to problem 3. For her, diminution of errors from series to series, beginning with the 5th, is unusually regular. Her solution was perfectly definite and decisive.

In view of the widely differing motivational conditions for the four subjects (electrical stimulus not used for Mamo) and the previously demonstrated differences of the several subjects in adaptiveness, temperament, and success in the multiple-choice experiment, the range of trials necessary for solution of problem 3 (120 to 160 trials) is surprisingly narrow. It indicates that the problem of the right-end mechanism may safely be rated as fairly easy for chimpanzees.

To compare the statistical results of problem 1, the left-end mechanism, with those of problem 3, the right-end mechanism, would be futile because of the experience in problem 2 which intervened between solution of problem 1 and presentation of problem 3. Beyond doubt, the prolonged and withal extremely discouraging work in problem 2 profoundly, and in many ways, modified the reactive tendencies, and probably also the capacities, of the subjects. Possibly if either problem 2 or problem 3 had been presented initially instead of problem 1, as the first multiple-choice problem for these subjects, it would have proved considerably easier of solution than problem 1 by reason of the subjects' very marked preference for mechanisms toward the right side of the apparatus.

Of the utmost importance is the fact that, following solution of problem 3, as was also the case in problem 1, every one of the subjects responded perfectly and with evident ease and satisfaction to the series of control settings. Coupled with varied other evidences, this in my opinion proves that in the end-box problems (nos. 1 and 3) the subjects depended for their success not upon characteristics of the particular setting or upon the uniform order of presentation of the settings, but instead upon the relationship which we should naturally describe as left-endedness or right-endedness. It is important to inquire and to seek to discover how, if at all, this relationship is represented or symbolized in the behavioral system of chimpanzee. Various investigations now in progress in these laboratories are directed toward the solution of this problem.

Before passing to consideration of other aspects of the behavior of the subjects in their solution of problem 3, the results of re-presentation to Mamo will be examined. It will be recalled that she successfully solved this problem in July, 1932. After a rest period of nearly eight months, the problem was re-presented to her under somewhat different motivational conditions, in that the apparatus had been electrified and mistakes were penalized by electrical stimulation. Probably almost any investigator experienced in behavioral work with mammals would have predicted that on re-presentation she would either exhibit perfect adaptation to the problem or very quickly re-adapt. What actually happened is indicated below in terms of responses and errors per series.

TRIALS	RESPONSES	ERRORS	TRIALS	RESPONSES	ERRORS
1–10	35	9	91–100	13	3
11–20	27	8	101–110	17	7
21–30	20	8	111–120	13	3
31–40	19	8	121–130	15	5
41–50	19	8	131–140	12	2
51–60	17	7	141–150	12	2
61–70	17	7	151–160	12	2
71–80	17	6	Control	13	3
81–90	15	5	161–170	12	2
			Control	14	4

In the 160 trials which Mamo was given while the other subjects were working out their solutions of problem 3, she progressed much as on original presentation of the problem from degree of success indicated by 10 per cent correct responses to 80 per cent in her 16th series. It was decided thereupon to terminate this review experiment by presenting the control series. As in case of the regular series, she failed to adapt.[4] In her first control series she made three errors, and in a second, four.

The above results would be the more surprising had not Mamo been used for continuation work on problem 2 just prior to the review presentation of problem 3. It is regrettable that problem 3 was not presented at the beginning of the season, instead of following problem 2.

Values, in problem 3, of reaction boxes, settings, and size groups, comparable with those already presented for problems 1 and 2, appear in tables 17–19.

Again it is to be remarked that the difficulty of boxes at the right end of the apparatus is greater than of those at the left end.

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[4] She was required to choose until she entered the correct box.

Since box 9 when used was always correct by definition of the problem, it is peculiarly surprising that Al should have persistently avoided it in favor of box 8, which, statistically viewed, is the most difficult of all of the mechanisms. These results of table 17 are of interest primarily by comparison with the corresponding ones for problem 1 as presented in table 6, p. 19.

TABLE 17

Relative difficulty of boxes (1–9) in problem 3

SUBJECTS	BOXES								
	1	2	3	4	5	6	7	8	9
Average number of incorrect responses per box for all settings									
Bentia	.000	.161	.357	.268	.250	.086	.411	.750	.000
Soda*	.042	.094	.344	.156	.000	.000	.219	.875	.000
Al†	.021	.281	.469	.297	.281	.075	.204	.969	.000
Mamo	.146	.297	.344	.250	.219	.200	.391	.625	.000
Average	.052	.208	.379	.243	.188	.090	.306	.805	.000
Order of increasing difficulty of boxes (by number) for the ten settings combined									
Bentia	1	6	2	5	4	3	7	8	0
Soda*	5 =	6	1	2	4	7	3	8	0
Al†	1	6	7	2 =	5	4	3	8	0
Mamo	1	6	5	4	2	3	7	8	0
Combined order	1	6	5	2	4	7	3	8	0

* Trials 1–40 omitted.

† Irregular—Al did not make perfect score. Trials 151–160 treated as perfect series.

As to the difficulty of settings (table 18), especially worthy of consideration is the altogether convincing indication that the several settings vary from easy to difficult for the individual subjects.

When difficulty of settings is viewed in relation to number of mechanisms in use, that is, size of group, it is apparent from the data of table 19 that the number of trials necessary for adaptation to a particular setting tends to vary directly with the size of the group. Whereas two-box settings required on the average eight

TABLE 18

Relative difficulty of settings in problem 3

SUBJECTS	SETTINGS									
	1 5-6	2 6-8	3 1-3	4 4-9	5 6-8	6 2-4	7 3-7	8 1-2	9 2-5	10 1-9
Number of trials per setting prior to disappearance of errors										
Bentia	10	10	6	12	10	8	10	0	12	13
Soda*	0	3	5	4	0	7	0	5	7	6
Al†	12	12	11	13	11	13	12	11	11	16
Mamo	12	11	15	6	12	14	15	14	11	13
Average	8.5	9.0	9.3	8.8	8.3	10.5	9.3	7.5	10.3	12.0
Total number of responses per setting prior to disappearance of errors										
Bentia	21	19	8	25	19	16	24	0	41	26
Soda*	0	6	7	16	0	14	0	6	17	12
Al†	22	16	15	30	16	30	39	12	43	35
Mamo	18	19	33	13	22	36	28	18	20	55
Average	15.3	15.0	15.8	21.0	14.3	24.0	22.8	9.0	30.3	32.0
Number of correct first responses per setting to and including first perfect series										
Bentia	5	5	12	3	5	6	5	14	2	4
Soda	8	6	6	5	8	2	8	7	2	3
Al†	6	13	13	3	11	7	7	15	5	0
Mamo	10	8	2	10	9	4	8	12	8	6
Average	7.3	8.0	8.3	5.3	8.3	4.8	7.0	12.0	4.3	3.3
Order of increasing difficulty of settings (by number) as derived from above data										
Bentia	8	3	6	2 =	5	1	7	4	10	9
Soda*	1 =	5 =	7	2	8	3	4	10	6	9
Al†	8	3	5	2	1	6 =	7 =	9	4	10
Mamo	4	1	8	2	9	5	7	10	6	3
Average	8	1 =	5	2	3	7	4	6	9	10
Number of correct first responses per setting without interruption to and including first perfect series										
Bentia	4	4	8	2	4	6	4	14	2	1
Soda	8	5	3	4	8	1	8	3	1	2
Al†	4	4	5	3	5	3	4	5	5	0
Mamo	4	5	1	10	4	2	1	2	5	3
Average	5.0	4.5	4.3	4.8	5.3	3.0	4.3	6.0	3.3	1.5

* Trials 1–40 omitted.

† Irregular—Al did not make perfect score. Trials 151–160 treated as perfect series.

trials, the nine-box setting required twelve, and whereas for two-box there were 9.6 correct responses, for nine-box there were only 3.3. These differences unquestionably are significant and they must be carefully considered in attempts to evaluate the data on responses and errors and to determine dominant reactive tendencies and modes of problem solution. Only one setting, 6–8, was repeated in the problem 3 series. According to the data of table 18, the subjects succeeded little better on second presentation of this setting than when it first appeared.

TABLE 19

Relative difficulty of size-groups of box settings for problem 3 as indicated by number of trials and successes

SUBJECT	NUMBER OF BOXES IN SETTING					
	2 (2 settings)	3 (4 settings)	4 (1 setting)	5 (1 setting)	6 (1 setting)	9 (1 setting)
Number of trials for solution (disappearance of errors)						
Bentia	5.0	8.5	12.0	10.0	12.0	13.0
Soda*	2.5	3.8	7.0	0.0	4.0	6.0
Al†	11.5	11.8	11.0	12.0	13.0	16.0
Mamo	13.0	13.0	11.0	15.0	6.0	13.0
Average	8.0	9.3	10.3	9.3	8.8	12.0
Number of correct first responses per setting to and including first perfect series						
Bentia	9.5	7.0	2.0	5.0	3.0	4.0
Soda*	7.5	5.5	2.0	8.0	5.0	3.0
Al†	10.5	11.0	5.0	7.0	3.0	0.0
Mamo	11.0	5.8	8.0	8.0	10.0	6.0
Average	9.6	7.3	4.3	7.0	5.3	3.3

* Trials 1–40 omitted.

† Irregular—Al did not make perfect score. Trials 151–160 treated as perfect series.

One important result of the gradually perfected general adaptation of my subjects to the multiple-choice apparatus and procedure was marked lessening in time of response. It required on the average, and apart from the time necessary for transfer of the animals, recording of results and note-taking, less than half as long for the actual responses of the subjects in problem 3 as in problem 1. To serve the double purpose of exhibiting this relationship, and also providing a sample detailed time record, the average time per trial for each of the four subjects in problems 1 and 3 is presented in table 20.

The time of a trial was taken by starting a stop watch at the instant the subject was admitted to response compartment *B* and stopping the watch when the subject was released from the correct box to alley *C*. An exception to this rule was made in case of direct and immediate correct responses, when the time for each was always recorded as five seconds.

Individual differences were particularly conspicuous in the response of the several subjects to the change in the apparatus due to electrification, and also in response to the electric stimulus as penalty for mistakes. Bentia was not greatly affected either by the change in apparatus or by the novel experience of electrical stimulus. Still less was she disturbed or disconcerted. Initially she barely noticed the electrodes. Promptly she accepted them as part of the situation. From the first she either failed to respond definitely and in such manner that it could be attributed to the electric shock, or without particular haste or evidence of annoyance avoided or withdrew from it. These statements of course apply only to shocks of moderate strength, for in later experiments it was demonstrated that when the strength of stimulation was markedly increased, she exhibited emotional disturbance and inhibition of response.

By contrast with Bentia, Soda was quite upset by the electrification of the apparatus. She was fearful of the electrodes, and it required several days so far to re-adapt her to the apparatus that she would enter and pass through the reaction boxes in her usual manner. Gradually she became accustomed to the new conditions, and within a week she was reacting naturally. Lest it be assumed that her behavior was determined by the electrical stimulus, it should be especially emphasized that the above statement applies strictly to the change in apparatus. The electrical stimulus was not used with Soda until she had become

TABLE 20

Average time of trial per series

TRIALS (BY 10'S)	BENTIA		SODA		AL		MAMO	
	P. 1	P. 3	P. 1	P. 3	P. 1	P. 3	P. 1	P. 3
1–10	288.5″	24.7″	13.7″	—*	143.6″	18.7″	247.6″	11.8″
11–20	181.1″	16.3″	62.7″	—*	25.0″	20.1″	199.1″	11.2″
21–30	100.8″	11.0″	9.6″	—*	11.5″	13.8″	20.0″	20.2″
31–40	71.9″	14.7″	15.8″	—*	22.6″	13.6″	22.4″	17.1″
41–50	22.4″	10.1″	14.1″	35.8″	13.1″	14.0″	13.3″	16.0″
51–60	62.4″	28.0″	14.4″	27.0″	25.6″	15.1″	17.7″	14.9″
61–70	58.2″	13.8″	12.5″	18.0″	14.6″	19.8″	17.5″	11.7″
71–80	33.0″	14.9″	19.1″	20.4″	18.7″	13.2″	17.2″	7.3″
81–90	55.7″	11.9″	8.9″	10.6″	17.7″	13.4″	11.6″	5.9″
91–100	54.4″	11.4″	10.7″	7.5″	14.0″	16.4″	12.6″	16.0″
101–110	61.9″	6.6″	11.2″	6.7″	15.1″	19.0″	12.9″	12.3″
111–120	94.2″	7.4″	10.3″	5.6″	13.1″	9.4″	10.6″	20.1″
121–130	34.0″	6.5″	16.7″	5.8″	12.0″	8.5″	9.9″	14.1″
131–140	21.8″	7.1″	12.5″		11.8″	7.9″	9.2″	9.4″
141–150	23.1″	6.3″	17.1″		12.4″	8.1″	7.5″	10.8″
151–160	26.7″		13.1″		14.5″	8.2″	8.8″	5.3″
161–170	32.1″		8.8″		9.8″		7.4″	5.0″
171–180	12.2″		5.3″		8.1″		10.6″	
181–190	17.0″				5.5″		13.0″	
191–200	14.9″						10.8″	
201–210	40.4″						12.0″	
211–220	57.2″						13.6″	
221–230	46.5″						17.5″	
231–240	25.3″						17.0″	
241–250	17.5″						15.2″	
251–260	24.4″						14.1″	
261–270	21.9″						15.0″	
271–280	19.7″						13.3″	
281–290	30.2″						13.5″	
291–300	32.0″						8.7″	
301–310	24.2″							
311–320	24.7″							
321–330	41.1″							
331–340	17.0″							
341–350	25.9″							
351–360	18.9″							
361–370	25.1″							
371–380	39.8″							
381–390	16.8″							
391–400	22.2″							
401–410	6.3″							
Control...	5.2″	5.6″	5.4″	5.3″	5.5″	9.3″	7.8″	5.0″
Control...		6.5″	5.6″	5.0″	5.3″	8.8″		5.0″

* Electrification—aided.

accustomed to the electrodes. To it she responded much more markedly than did Bentia. It is my impression that she also was more sensitive, but certainly she was very much more expressive, more apprehensive of the shock, and more persistently intent on avoiding it, whatever its strength. It became her habit, the instant she entered one of the boxes and whether or not electrical stimulus was received, to climb to the top of the box and there, safe from electrical stimulation, to await the opening of either the exit door or the entrance door.

Al noticed but was only slightly disturbed by the change in the apparatus due to electrification. Very quickly he took it as a matter of course. The same statement applies to electrical stimulation. At first he seemed mildly surprised and interested. In common with the other subjects he examined the novel aspects of the apparatus and searched for the source of the new experience. Often it was extremely difficult for O to be certain that he was stimulated. Probably he was little if any more sensitive than Bentia; most likely less so than Soda and Mamo. Yet it is by no means certain that difference in sensitivity is even primarily responsible for the marked difference in responsiveness to electrical shocks which these four subjects exhibited. Not until the stimulus had been increased in strength in a degree which was painful to the experimenter did Al respond with extreme vigor and exhibit resentment, determination to avoid the stimulus, and pronounced inhibition of response.

Mamo, when confronted with the electrification situation, noticed and casually examined it. She was not considerably disturbed, nor, on the other hand, was she willing to ignore the changes or accept them immediately as part of the situation. The shock from the first interested her and quite evidently stirred her curiosity, for she examined its immediate source in the floor of the boxes carefully and repeatedly. There was seldom doubt about reception of the stimulus in her case, for she responded definitely, although usually not with extreme vigor. Relatively early she developed an effective method of avoiding or minimizing electrical stimulation. She hopped into the box so that only one or two extremities touched the floor and electrodes.

Then, and as quickly as possible, she removed all extremities from the electrodes either by crowding into the far end of the box or climbing up from the floor. Her peculiar method of skipping into the box instead of walking in usual fashion on hands and feet was amusing to watch and suggested playfulness rather than serious utility.

I had anticipated varied difficulties and embarrassments in the utilization of electric shock as inhibitor of incorrect response and as general motivational factor. In this I was disappointed, for from the first the chimpanzees accepted the electric stimulus without resentment or inhibition. It was peculiarly advantageous that they did not refer it to the experimenter. Not until trial was made of relatively strong stimuli did interference with prompt response appear. It may fairly be stated that the electric stimulus as motivational condition proved eminently satisfactory in this experiment so far as convenience of use and relation to the behavior of the organism are concerned. That it had any considerable value as factor affecting solution of multiple-choice problems is not evident. On the contrary, I have the impression that neither factors which tend motivationally to reënforce correct responses nor those which tend similarly to inhibit incorrect responses are of primary importance to chimpanzee in the discovery of the cue necessary to perfect adaptation.

Relative to systematizations of behavior exhibited in connection with problem 3, there are a few significant generalizations. The previous problems pronouncedly affected in several and conspicuous ways response to problem 3 and the time of its solution. This applies especially to reactive tendencies relative to boxes, settings, and the order of settings. As has been stated before, it is not simply or merely a matter of responding to a particular mechanism or a particular group of mechanisms, with determination of response by the immediate characteristics of mechanism or group, but instead of being influenced by what has preceded this particular presentation, not merely in the immediately prior setting or settings, but as well in previous problems. In addition to a reaction pattern for a given setting or multiple-choice problem, there is a constellation of reactive tendencies or patterns whose mutual relations in the main determine the immediate adaptive response of the subject. Furthermore, it is strongly suggested by the responses and statistical data for problems 1, 2, and 3, that abruptness or suddenness of solution depends primarily on the difficultness of the problem. The easier the problem, the more likely sudden discovery of the essential relationship. Reënforcement, inhibition, conflict, attention, are manifestly important in connection with the appearance, functioning, and disappearance of systematizations or transient modes of response, and upon them depend the rate and perfection of adaptation.

Few readily identifiable and persistently used systematizations appear in the records for Bentia in problem 3. She chose the left-end mechanism relatively seldom and there were few repetitions of response and perseverations. Naturally, the box second from the right end was frequently chosen in most settings. Of settings consisting of two boxes in the problem 3 series, 1–2 was responded to correctly from the first, whereas 5–6 was persistently responded to by choice of box 5. Perhaps problem 3 was rather too easy to develop systematizations. At any rate, errors after trial 100 were few and limited to the box second from the right end, which as error is referable to experience in problem 2. There are no systematizations of particular interest or novelty in the records for Soda. Naturally for her, as well as for the other subjects, the effects of previous training in selection of the left-end mechanism or of the mechanism second from the right end appeared. Al exhibited at times preference for the second from the right end and less frequently for other intermediate boxes. The 10th setting, 1–9, as previously stated (p. 46), was peculiarly difficult for him and with remarkable persistence he chose box 8 instead of 9. Mamo exhibited marked dominance of the second box from the right and persistence of tendency to choose on the basis of her experience in problem 2. This is significant inasmuch as she had such great difficulty in solving problem 2. She made no other errors than second from right choices after her 14th series. Interestingly enough, by contrast with the results for Al, Mamo had no special difficulty with setting 10, boxes 1–9. Distinctive of the responses of Mamo was the reappearance of errors, from time to time, in several settings after they apparently had been mastered.

Types of solution for the problem of right-end box are indicated by the content of table 16, and in connection therewith it has been suggested (p. 44) that relatively abrupt or sudden discovery of the relationship occurred in case of Bentia, Soda, and Al, whereas Mamo's solution came slowly and by gradual elimination of incorrect types of response. The composite error curve for this problem, presented herewith as figure 6, represents gradual reduction of errors and suggests not at all sudden discovery of the relationship of right-endedness.

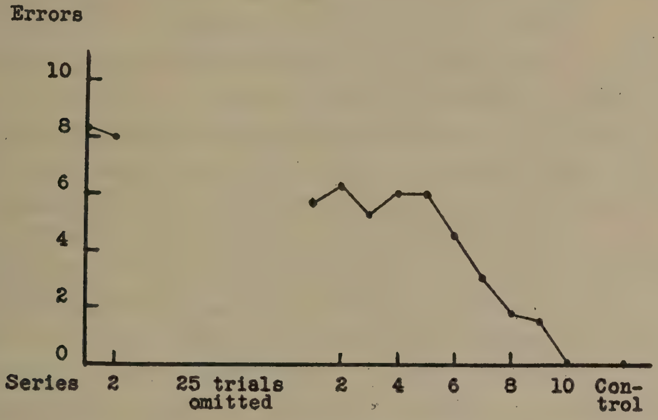

Fig. 6. Composite Error Curve for All Subjects (4) in Problem 3, Right-end Box

Average errors for the first two and the last ten series are presented. The statistical data appear in table 16. There were no errors in control series.

CONDITIONS AND RESULTS FOR PROBLEM 4, MIDDLE BOX

As fourth problem that of the middle mechanism was used. In view of previous experience with other mammals, it was assumed that this problem would be soluble by chimpanzee, but certainly with much greater difficulty than problems 1 and 3. Aside from necessary adaptations to individual characteristics and reactive status, conditions of experimentation were the same for all subjects and in general as described below.

As distinctive symbol of the problem, by which in later work the subjects might be able to identify it, a conspicuous new feature was introduced in the apparatus. It consisted of a $\frac{7}{8}$-inch board, 14 cm. wide, painted black, which extended across the front of the bank of boxes. The lower edge of the board was 77 cm. from the lower front edge of the boxes and 105 cm. from the ground. This strip of black was extremely conspicuous and could scarcely be overlooked by the subject. The purpose of the experimenter in introducing it was later to determine the ability of a subject, which had mastered this among other multiple-choice problems, to identify the problem by its symbol and to respond properly, although perhaps on the previous day it had been working on a quite different problem.

Each subject was used alone for work in problem 4. One series of 10 trials was given each day without exception. Food was used regularly as reward of completed trial. In trials 1–100 it was presented at *R*; thereupon, and for trials 101–300, it was presented instead in the appropriate cup at end of correct box. This change was made to discover whether closer association of the reward, temporally and spatially, with success in passing through the apparatus to alley *C* and thus obtaining food, would render possible or facilitate problem solution. As previously, fruits were generally used as rewards and each subject received in the course of its series of trials at least the equivalent of one orange and one banana or one-half grapefruit and one banana.

With the exception of the last few series in this problem, the subject, after five mistakes in a trial, was aided by O in locating the correct box. As previously, this was done by unlocking the exit door and as necessary moving it slightly. To supplement the positive or reënforcing values of rewards for correct response, two forms of punishment were used, sometimes separately and again in combination, as inhibitors of incorrect responses. In the first three series mistakes were not penalized and the entrance door was not lowered until the correct box had been selected. In the 4th series, trial 31, the first mistake in a trial was punished by electrical stimulation. In the following series the first two mistakes were punished. The strength of stimulus was varied in accordance with individual responsiveness. For Bentia and Al it ranged from coil setting 4 to 2, the latter producing over-stimulation; for Soda and Mamo, from 5 to 3. It was necessary to use the shock cautiously and not too frequently. In general, it proved unsatisfactory to penalize mistakes regularly by strong electrical stimulation.

As the subjects failed to exhibit consistent improvement or evident approach to problem solution during the first 200 trials, it was decided to attempt to aid them in the discovery of the relationship by setting the doors differentially. This was done beginning with the 21st series, trial 201, for which the correct door was raised to a height of 75 cm., whereas all other open doors were placed at 50 cm. To test promptly the effect of the distinctive visual appearance of the correct door, regular series of trials, with all doors set at approximately 70 cm., were alternated with series of differential settings. This phase of the experiment was continued from trials 201 to 300.

From trial 301 to the end of the experiment, regular 70 cm. settings and punishment by 30 seconds confinement for first mistake in one series and electrical stimulation in the next were used.

Because no one of the subjects, although all were working patiently and apparently with maximal effort, had exhibited consistent improvement in response to the situation or given definite promise of solution, work was discontinued with the 400th trial. Decision to abandon the problem at this point was based chiefly upon the discouraging and complicating effects of long continuation of work on problem 2. On the whole, it seemed wiser to proceed to other and radically different sorts of relational problem than that of middleness, with the hope that some at least of the subjects might achieve perfect adaptation.

The records for this problem indicate not only that all of the subjects wholly failed to adapt, but that practically as many errors per series were made in the last 50 trials (351–400) as in the second 50 (51–100). The averages for three significant points in the array of results are presented herewith. Naturally, errors in the first 50 trials were due in considerable measure to immediately prior experience in problem 3 and the acquired tendency to choose the right-end box. The second 50 and the last may fairly be compared, and it is significant that Bentia and Mamo made more errors per series late than early, Soda and Al somewhat less.

TRIALS	NUMBER OF ERRORS			
	Bentia	Soda	Al	Mamo
1–50	7.4	8.6	9.0	8.0
51–100	6.0	6.6	8.4	5.2
351–400	6.8	5.6	5.8	6.6

Referring to the records of responses and errors for the 40 series, as given in table 21, it is evident that during the first 200 trials no one of the animals consistently reduced frequency of responses or errors. There was, as a matter of course, marked reduction in every case during the early series in which the effects of previous training were in process of eradication, but as between the 6th series and the 20th, there is nothing in the results to justify prediction of problem solution.

Neither the behavior of the subjects nor the statistical data of tables 21 and 21a indicate advantage of placement of reward in cups versus at *R* in alley *D*. Reliable differences are lacking in the response and error data of table 21a. The results are presented by groups of 100 trials to facilitate part comparisons. Reward was remote (at *R*) for trials 1–100 and 301–400; it was near (in cups) for trials 101–200 and 201–300. Trials 1–100 should be excluded because they exhibit initial adaptation under the influence of the previous problem, with consequent high frequency of responses and errors. Trials 201–300 should be excluded because for them the doors were set differentially and correct response thus facilitated. Comparison of trials 101–200 (near reward) with 301–400 (remote reward) is legitimate. It is not indicated by the data for responses and initial errors that either placement of reward was more favorable than the other. Possibly neither condition affected the results because adaptation was lacking and the subjects were responding, in effect, to an

TABLE 21

Number of responses and number of initial errors per series of ten trials in problem 4, middle box

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
1–10	37	8	33	9	44	9	36	9
11–20	35	8	33	8	35	8	43	9
21–30	31	8	33	9	43	9	40	7
31–40	27	7	29	8	37	9	43	9
41–50	30	6	37	9	40	10	31	6
51–60	26	6	29	7	35	8	35	5
61–70	23	6	25	7	37	9	28	5
71–80	20	4	22	6	35	8	37	7
81–90	22	6	21	6	34	9	26	4
91–100	25	8	25	7	31	8	33	5
101–110	27	8	20	6	27	7	35	7
111–120	26	7	24	6	33	8	31	5
121–130	26	7	21	6	24	8	20	5
131–140	27	8	28	8	30	6	27	6
141–150	20	5	24	7	26	8	28	6
151–160	25	9	19	4	29	8	35	8
161–170	25	7	16	3	21	7	31	7
171–180	27	8	25	4	23	7	29	6
181–190	15	5	19	4	27	6	29	6
191–200	25	9	22	5	18	6	26	5
201–210	18	4	16	2	13	2	28	6
211–220	11	1	13	1	21	4	19	4
221–230	19	4	16	5	22	7	19	5
231–240	11	1	10	0	20	5	18	2
241–250	22	6	14	3	21	6	13	2
251–260	10	0	10	0	11	1	15	2
261–270	22	8	22	6	18	5	25	4
271–280	57*	10	35*	10	41*	10	34*	9
281–290	16	4	16	2	26	2	16	4
291–300	29	10	26	10	47*	10	30	9
301–310	32	8	21	5	28	6	22	5
311–320	22	8	24	7	31*	6	29	4
321–330	26	7	25	6	28	5	17	4
331–340	23	8	17	2	20	7	31	7
341–350	34	7	25	4	42	8	36	6
351–360	20	6	21	5	27	5	14	3
361–370	19	6	31	5	22	6	27	4
371–380	31	7	24	7	30	6	25	9
381–390	25	8	22	6	22	7	22	9
391–400	19	7	22	5	24	5	40	8

* Exact record not made of all doors entered after first five.

In trials 201–300 the doors were set differentially.

insoluble problem. It may not safely be inferred from these negative results that temporal and spatial relations of reward to the correct reaction mechanism are always unimportant in the box multiple-choice experiment.

TABLE 21a

Number of responses and number of errors per one hundred trials in problem 4

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
1–100	276	67	287	76	371	87	352	66
101–200	243	73	218	53	258	71	291	61
201–300	215	48	178	39	240	52	217	47
301–400	251	72	232	52	274	61	263	59

Requiring special examination and discussion are the results for trials 201–300, in which differential door settings were used in an experimental effort to exhibit to S the essential relationship of the correct mechanism. The precise conditions for the 10 series which constitute this special experiment are indicated herewith.

Trials	*Conditions*
201–210	Correct door at 75 cm.; all other doors at 50 cm.; first mistake punished by electrical stimulation
211–220	Same
221–230	Regular setting of doors, 70 cm.; punishment as previously
231–240	Differential setting of doors 75 cm. versus 50 cm.; punishment as previously
241–250	Regular setting of doors, 70 cm.; electrical stimulus increased
251–260	Differential setting of doors 75 cm. versus 50 cm.; strong electrical stimulation
261–270	Regular setting of doors, 70 cm.; punishment as previously
271–280	Reversal of sign: correct door at 40 cm., other doors at 65 cm.; punishment as above
281–290	Regular setting of doors, 70 cm.; diminished strength of electrical stimulation
291–300	Differential setting, 50 cm. versus 65 cm.; no electrical stimulation; confined 30″ for first mistake.

The above described differential setting of the doors served immediately to reduce the number of responses and errors, and, as appears in table 21, in trials 211–220 Bentia and Soda made a single error each, Al and Mamo four errors each. When, however, in the next series the subjects were confronted with the regular 70 cm. setting of all doors, the errors increased for each subject, Bentia exhibiting the best record with four errors. Again under the differential conditions of series 24, Bentia's errors were reduced to one, Soda achieved a perfect series, Al made five mistakes, and Mamo two only. Once more, presentation of the regular settings of the doors in series 25 proved that Bentia and Al had not profited by the experimenter's attempt to aid them, whereas Soda and Mamo apparently had to a certain degree, since their errors stood three and two respectively. For the differential settings of series 26, trials 251–260, table 21 shows perfect response on the part of Bentia and Soda, a single error for Al, and two for Mamo. Lack of transfer of primary effects of the differential setting is demonstrated again by series 27, in which the number of errors ranges from eight for Bentia to four for Mamo. Reversal of the differential sign in case of series 28 very naturally upset the subjects, for they were misled. They made a great many mistakes of choice, were initially wrong in every trial, with the exception of Mamo, who had one success, and except for aid from the experimenter they undoubtedly would have been completely discouraged by the situation and possibly would have quit work. It is especially noteworthy that on presentation of the regular settings in series 29 following the extremely disturbing effects of sign reversal, all of the subjects did unusually well. Failure appears again in series 30, and subsequently in the succeeding regular settings.

In summarizing the results of this experimental attempt to facilitate discovery of the relationship of the correct mechanism to its companion mechanisms, it suffices to say that there is no evidence of positive value. Rather quickly the subjects perceived the distinctive appearance of the correct mechanism and chose it with high frequency, but within the limits of this experiment the advantage thus gained did not transfer to the regular series of settings in which all open doorways were visually similar.

In the latter part of the work on problem 4, over-stimulation electrically caused certain irregularities, inhibitions, and even un-willingness to come to the apparatus and extreme reluctance to work. In every case such untoward developments were promptly remedied by cessation of punishment and encouragement of the subjects to work for the reward of food.

The observer's comment on the content of table 21 may be concluded, as it began, with the statement that to judge by the statistical data of responses and errors, the subjects were as remote from discovery of the essential relationship and resulting perfect adaptation to problem 4 at the end of 400 trials as at the beginning of their work. If in this connection "learning" may properly be spoken of, the process seemingly had not been initiated, and there is no evidence that in the course of training gradual adaptation to the situation by elimination of inadaptive acts occurred.

TABLE 22

Relative difficulty of boxes (1–9) in problem 4, trials 1–200

SUBJECTS	BOXES								
	1	2	3	4	5	6	7	8	9
Average number of incorrect responses per box for all settings									
Bentia	.017	.213	.420	.313	.330	.440	.690	.600	.350
Soda	.000	.175	.250	.300	.370	.550	.520	.770	.263
Al	.017	.113	.370	.400	.500	.650	1.160	.970	.275
Mamo	.133	.275	.230	.288	.770	.620	.820	1.020	.550
Average	.042	.194	.318	.325	.493	.565	.798	.840	.360
Order of increasing difficulty of boxes (by number) for the ten settings combined									
Bentia	1	2	4	5	9	3	6	8	7
Soda	1	2	3	9	4	5	7	6	8
Al	1	2	9	3	4	5	6	8	7
Mamo	1	3	2	4	9	6	5	7	8
Combined order	1	2	3	4 =	9	5	6	7	8

The data indicative of relative difficulty of boxes, settings, and size-groups are important in comparison with those for the foregoing problems. In case of problem 4, the end box 9 proved relatively very much easier than previously, and except that it falls in the middle of the series, the order of increasing difficulty

TABLE 23

Relative difficulty of settings in problem 4

SUBJECTS	SETTINGS									
	1 2–4	2 5–9	3 1–7	4 7–9	5 4–8	6 1–9	7 1–3	8 2–6	9 3–9	10 6–8
Total number of responses per setting in 40 series										
Bentia	58*	89	132	70	111	178	47	90	142	68
Soda	66	105*	102*	55	99	163*	61	83	127	54
Al	70	96	167*	70	109	236*	81	113	132	69
Mamo	64	106*	176	53	146	200	42	136	141*	59
Average	64.5	99.0	144.3	62.0	116.3	194.3	57.8	105.5	135.5	62.5
Number of correct first responses per setting in 40 series										
Bentia	25	16	9	11	10	3	33	11	9	13
Soda	26	20	15	25	11	3	19	21	10	30
Al	19	12	9	12	17	0	7	17	13	17
Mamo	27	12	6	30	9	4	38	7	4	30
Average	24.3	15.0	9.8	19.5	11.8	2.5	24.3	14.0	9.0	22.5
Order of increasing difficulty of settings (by number) as derived from above data										
Bentia	7	1	10	2	4	8	5	3	9	6
Soda	10	4	1	7 =	8	2	3 =	5	9	6
Al	1 =	10	4 =	5	8	2	7 =	9	3	6
Mamo	7	4	10	1	2	8	5	9	3	6
Average	10	1	4	7	2 =	8	5	3 =	9	6
Number of correct first responses per setting without interruption										
Bentia	0	0	0	0	0	0	10	0	0	0
Soda	2	0	0	0	0	0	0	0	0	10
Al	0	0	0	0	5	0	0	2	5	0
Mamo	0	0	0	0	0	0	24	0	0	0

* Exact record not made of all doors entered after first five.

corresponds precisely with that of the numbered series of boxes, 1–9. It is interesting to ask whether had the escape alley and the delivery of food as reward been at the left instead of the right side of the apparatus, the order of box difficulty would have been correspondingly reversed. In the present investigation, opportunity did not offer for this particular modification of conditions of observation.

The reactive value of the various settings cannot be determined in case of problem 4 by application of the definitions of statistical data presented on page 15, inasmuch as the subjects failed to solve the problem within 400 trials. In only a few instances was any particular setting solved. The several determinations therefore have been made for the total number of series, 40, or in case of difficulty of boxes, for 1–20.

The data of table 23 show that there was extreme difference in difficulty among settings and also of the same setting for different individuals. For example, settings 7 and 1 were particularly easy for Bentia; settings 10 and 4, for Soda; settings 1 and 10, for Al; and for Mamo, settings 7 and 4.

TABLE 24

Relative difficulty of size-groups of box settings for problem 4

SUBJECTS	NUMBER OF BOXES IN SETTING			
	3 (4 settings)	5 (3 settings)	7 (2 settings)	9 (1 setting)
	Number of correct first responses per setting in 40 series			
Bentia	20.5	12.3	9.0	3.0
Soda	25.0	17.3	12.5	3.0
Al	13.8	15.3	11.0	0.0
Mamo	31.3	9.3	5.0	4.0
Average	22.7	13.6	9.4	2.5

It is indicated that in general the smaller groups were easier than the larger. This fact is definitely established by the data of table 24, which on the basis of number of initially correct responses for the size-groups 3, 5, 7, and 9 boxes show a regular and very marked increase in difficulty with size of group, for the correct responses in case of 3 were almost ten times as numerous as in case of 9. In no one of the problems previously presented was group size as important a factor in the determination of difficulty of adaptation as in the problem of middleness. It seems not improbable therefore, that had the size of groups been limited to 3, 5, or 7 mechanisms, or some combination of these numbers, the problem might have been solved by chimpanzee, for it is quite possible that the 9-group is beyond the capacity of the animal to survey and adapt to, and that its introduction in a series of settings causes confusion and thus prevents solution of the problem.

CONDITIONS AND RESULTS FOR PROBLEM 5, ALTERNATELY THE LEFT-END AND THE RIGHT-END BOX

Following the decisive, and to the experimenter wholly unexpected, failure of the chimpanzees in problem 4, it seemed desirable to present as the next problem one involving an entirely different principle of relationship than those previously used. With this in mind, alternation was selected, and problem 5 required the choice alternately of the left-end mechanism and the right-end mechanism in a given constant group of mechanisms. Undoubtedly the problem could have been rendered much more difficult by changing the setting of doors for each trial instead of continuing it in two successive trials.

As symbol of problem 5 the board previously described for use in the preceding problem, page 58, was used with its opposite side visible. It was painted white.

As general conditions of experimentation, the following are of special importance. Each subject was used alone throughout the experiment. A single series (10 trials) was given daily, with the exception that in trials 461 to 540, two series were given. All doors in the apparatus were regularly closed on the completion of a trial, and the doors for the next setting were opened after S had been returned to compartment *A* and was where the manipulation of the doors by O could be observed. As progress toward problem solution was not exhibited in the first two hundred trials, beginning with trial 201, and continuing until the end, time was economized by setting all intermediate doors so low that the boxes could not readily be entered. Initially the height of intermediates was 10 cm. and that of end doors 70 cm. Subsequently it was gradually increased to 45 cm. in an attempt to make the transition to the standard height of 70 cm. without having the subjects revert to choice of intermediates. In this I was unsuccessful. It is not indicated by the statistical results that differential setting of the doors rendered the problem easier. That it considerably reduced the number of incorrect responses is apparent from table 25. Thus the time required by the experiment was reduced.

At the beginning of this problem, the general adaptation of the subjects to the experimenter, apparatus, and procedure was perfect. Despite their varied difficulties and discouragements in connection with problems 2 and 4, they exhibited interest, coöperativeness, and as a rule eagerness to work.

The reward of food was varied in the course of the experiment both quantitatively and qualitatively. In certain series it was given regularly as previously described; in others, a relatively large quantity was given for initial successes and a relatively small quantity for incorrect trials. In yet other series, a preferred or positive food was offered in the former case and a disliked food in the latter. Mistakes were penalized either by punishment by confinement, which in duration ranged in the course of the experiment from approximately 10 seconds to a maximum of 60 seconds, by electrical stimulation, or, in a few series, by a combination of confinement and electrical shock. Among series in which punishment was used were interspersed a few for which reward alone was employed. So far as practicable the motivational conditions were the same for all subjects. In view of the results now to be presented, it appears unnecessary to describe the motivational conditions in greater detail and with reference to particular series.

Turning now to observational and statistical data, Soda, as a result of marked improvement in response which began with the 22d series, table 25, solved the problem rather abruptly in her 38th series. She was given two additional regular series on successive days to test the stability of her solution before presentation of the control settings. In the first supplementary series she made one error, in the second none. A subsequent control

TABLE 25

Number of responses and number of initial errors per series of ten trials in problem 5, alternately the left-end and the right-end box

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
1–10	51	9	66	9	119	9	91	8
11–20	49	9	44	9	87	10	46	6
21–30	46	10	38	10	64	9	40	6
31–40	54	10	43	9	42	10	40	8
41–50	34	10	33	6	35	8	31	9
51–60	31	8	37	5	59	10	54	10
61–70	30	6	32	6	28	9	27	8
71–80	33	7	24	4	27	6	25	6
81–90	23	4	31	7	26	7	35	6
91–100	34	8	26	6	34	8	29	8
101–110	46	7	25	6	29	9	21	5
111–120	22	4	27	6	22	7	19	4
121–130	31	7	21	5	24	7	18	5
131–140	24	5	23	5	29	8	18	5
141–150	44	8	28	6	25	6	20	5
151–160	42	8	27	6	29	7	23	4
161–170	27	7	20	8	27	7	21	5
171–180	29	8	30	6	16	4	26	7
181–190	22	5	25	6	28	9	37	9
191–200	24	7	21	6	31	8	22	9
201–210	17	6	16	4	18	6	17	7
211–220	16	6	16	2	15	4	16	6
221–230	14	4	15	4	15	5	15	5
231–240	16	6	15	4	17	7	16	6
241–250	17	7	15	5	16	6	17	7
251–260	13	3	15	4	15	5	14	4
261–270	14	4	13	3	17	7	18	7
271–280	12	2	13	3	16	6	17	5
281–290	16	6	12	2	16	6	15	5
291–300	17	7	13	3	13	3	14	4
301–310	17	7	12	2	16	6	15	5
311–320	16	6	12	2	13	3	15	5
321–330	13	3	11	1	13	3	17	6
331–340	18	7	11	1	14	3	15	5
341–350	17	7	14	3	23	9	15	5
351–360	14	4	13	3	13	3	16	6
361–370	13	3	13	3	13	3	16	6
371–380	14	4	10	0	14	4	15	5
381–390	13	3	11	1	15	5	16	5
391–400	15	5	10	0	14	4	15	5

TABLE 25—*Concluded*

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
Control...			10	2				
Control...			10	0				
401–410	13	3			15	5	15	5
411–420	13	3			14	4	16	6
421–430	14	4			15	5	15	5
431–440	13	3			15	5	13	3
441–450	14	4			12	2	15	5
451–460	13	3			14	4	14	4
461–470	15	5			14	4	15	5
471–480	15	5			13	3	16	6
481–490	15	5			15	5	14	4
491–500	13	3			15	5	15	5
501–510	15	5			13	3	12	2
511–520	12	2			15	5	16	6
521–530	16	6			15	5	13	3
531–540	13	3			13	3	14	4
541–550	14	4			15	5	13	3
551–560	15	5			15	5	15	5
561–570	12	2			15	5	13	3
571–580	14	4			13	3	13	3
581–590	12	2			15	5	11	1
591–600	14	4			14	4	13	3

series exhibited two errors, but a repetition of the series the following day yielded a perfect score.

For the successful individual, Soda, the order of difficulty of reaction mechanisms (table 26) is strikingly different from that of the previous problem. In the present instance, 1 replaces 9, and the latter appears to have been extremely difficult, whereas boxes 2, 3, 4, and 6 were appreciably easier than box 1.

There is nothing especially worthy of remark in the data for the several settings, table 27. As might naturally be expected, the relation of group-size to difficulty of a setting is less conspicuous than in problem 4. There is positive correlation, but it is relatively low. In table 28 the data for size-groups is presented not only for Soda, but in case of number of correct responses in 600 trials also for the three unsuccessful subjects, Bentia, Al, and

TABLE 26

Relative difficulty of boxes (1–9) in problem 5

SUBJECT	BOXES								
	1	2	3	4	5	6	7	8	9
Average number of incorrect responses per box for all settings									
Soda..............	.316	.202	.132	.267	.349	.305	.337	.491	1.105
Order of increasing difficulty of boxes (by number) for the ten settings combined									
Soda..............	3	2	4	6	1	7	5	8	9

TABLE 27

Relative difficulty of settings in problem 5

SUBJECT	SETTINGS									
	1 5–7	2 5–7	3 1–6	4 1–6	5 4–8	6 4–8	7 2–5	8 2–5	9 3–9	10 3–9
Number of trials per setting prior to disappearance of errors										
Soda.........	19	30	28	35	36	37	37	20	34	37
Total number of responses per setting prior to disappearance of errors										
Soda.........	41	60	60	95	98	85	67	38	179	70
Number of correct first responses per setting to and including first perfect series										
Soda.........	24	17	25	18	17	20	16	27	9	27
Order of increasing difficulty of settings (by number) as derived from above data										
Soda.........	8	1	3	2	10	4 = 6		7	5	9
Number of correct first responses per setting without interruption to and including first perfect series										
Soda.........	19	8	10	3	2	1	1	18	4	1

Mamo. For Soda there is no reliable difference in value of groups, and for the others individual variations are pronounced. On the average the six group is easier than the three.

This experiment was continued through 600 trials, and although responses and errors had diminished somewhat for Bentia, Al, and Mamo during their last 200 trials, the indication of improvement was so slight and so difficult to evaluate that it seemed wasteful of the experimenter's time to continue. True, Mamo in her 59th series made only one error, and Bentia in three of her late series had made only two errors. It is possible that all would have solved the problem perfectly if the experiment had been continued.

TABLE 28

Relative difficulty of size-groups of box settings for problem 5 as indicated by number of trials and successes

SUBJECT	NUMBER OF BOXES IN SETTING				
	3 (2 settings)	4 (2 settings)	5 (2 settings)	6 (2 settings)	7 (2 settings)
Number of trials for solution (disappearance of errors)					
Soda	24.5	28.5	36.5	31.5	35.5
Number of correct first responses per setting to and including first perfect series					
Soda	20.5	21.5	18.5	21.5	18.0
Number of correct first responses per setting in 60 series					
Bentia	28.5	36.0	19.0	43.0	12.5
Al	30.0	26.5	23.0	29.5	20.5
Mamo	30.5	27.0	27.5	27.5	26.0
Average	29.7	29.8	23.2	33.3	19.7

The error graph for the unsuccessful subjects in problem 5 is presented in figure 7 for comparison with that for pigs in their solution of the multiple-choice problem of alternate ends. Whereas the chimpanzee in 600 trials made only slight approach to adaptation, the pig acquired such adaptation gradually, as indicated by the curve, and with approximately 445 trials solved the problem.

Previously the experimenter had been greatly surprised by many features of the behavior of his chimpanzee subjects, and particularly by their inability to solve the problems presented. By the outcome of problem 5 he was again and more than ever amazed, partly because previous experience with other mammals had justified him in anticipating the ready mastery of the problem of alternate ends by chimpanzee, and also because the extensive use of the method of alternation or double alternation by Hunter and his associates (Hunter, 1928; Hunter and Nagge, 1931; Gellermann, 1931) made it appear that for various types of organism response by alternation is not extremely difficult.

It should be stated with emphasis that nothing appeared in the attitude, method of work, or special motivation of the successful subject Soda which serves to explain her adaptation to the problem by contrast with the failure of her companions. Every subject apparently did its best to succeed, and the outcome of effort, "discovery," seemed to be rather the result of a fortunate distribution and, at the proper instant, concentration of attention, than of more or less favorable motivation.

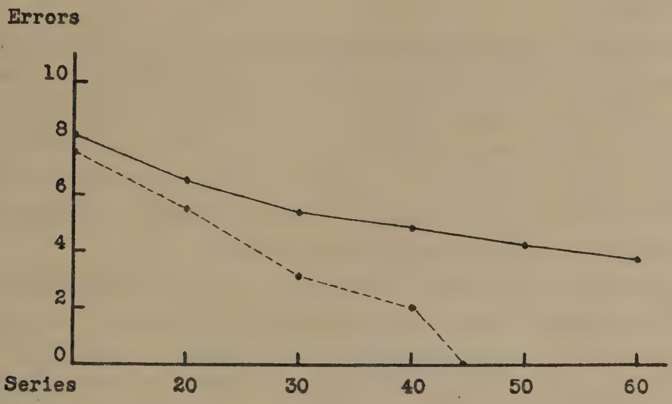

Fig. 7. Error Curves for Problem 5, Alternate Ends

Broken line, curve for pigs (2); solid line, curve for chimpanzees (3) which failed to solve problem in 600 trials.

CONDITIONS AND RESULTS FOR PROBLEM 6, THE SAME BOX

Like the problem of alternate ends, problem 6, the identical numbered mechanism in setting after setting, was selected on the basis of novelty of principle, but also with extreme ease as desideratum. The experimenter imagined that it might be adapted to very easily and quickly, and he wished especially to test this assumption.

The problem was presented to Soda in July, 1933, immediately after her solution of problem 5, and in September it was presented to Bentia, Al, and Mamo, and re-presented to Soda for review. In stating the conditions of experimentation, those obtaining for Soda in her initial solution of the problem will be given first, and, separately, the conditions for the subsequent work of all four subjects.

For this problem the symbol board presented during problems 4 and 5 was removed from the apparatus. Each subject was used alone.

For Soda a single series was given each day, with the exception of trials 21–100, which were given at the rate of two series per day. Food was regularly presented at *R* as reward. In the first 10 series mistakes were not penalized; in the 11th series the entrance door was closed for each mistake and the subject was confined for 10 to 15 seconds. In the 13th series confinement was increased to 30 seconds, and so continued.

By contrast with the above, the problem later was presented to all subjects under the following conditions. Reward, regularly at *R*. No punishment for mistakes in the first 5 series; punishment by closing of entrance door for each mistake and confinement from 5 to 10 seconds beginning with the 6th series. Electrical stimulation was not used.

The results of this experiment are strikingly different from those of the foregoing problems, and extraordinarily interesting. Soda was completely baffled by the situation and for a week, through 130 trials, showed no decrease in errors. In her 14th series, without any warning, she responded perfectly; so also in her control series. Like statements apply to Al and Mamo, with the important modification that their adaptation came very much more promptly, as abruptly, and to the experimenter as unexpectedly.

The composite error curve for this problem, based upon the error data of table 29, represents, I believe, abrupt discovery of the cue to success as contrasted with gradual adaptation through elimination of inadaptive responses.

The results of the several control series recorded in table 29 require special comment because of unusual conditions of presentation. In the midst of Bentia's control series on October 1 a sudden shower upset her emotionally and distracted her. Work was discontinued, and after the shower she was returned from her cage to the apparatus at about 11 o'clock. When taken from the cage she screamed in protest, and in the apparatus she seemed apprehensive and worried. Altogether both internal and external conditions seemed unfavorable, and the fact that two errors were made is not surprising.

TABLE 29

Number of responses and number of initial errors per series of ten trials in problem 6, same box (5)

TRIALS	BENTIA		SODA		AL		MAMO	
	Responses	Errors	Responses	Errors	Responses	Errors	Responses	Errors
1–10	26	6	32	7	32	7	42	8
11–20	19	4	32	7	40	10	27	5
21–30	19	7	33	7	24	7	27	7
31–40	16	5	21	5	22	8	17	5
41–50	16	3	22	6	17	6	31	6
51–60	15	3	16	5	17	4	22	4
61–70	10	0	14	4	10	0	20	6
71–80	10*	0*	18	5			23	6
81–90			25	7			19	5
91–100			28	8			10	0
101–110			17	6				
111–120			17	7				
121–130			17	6				
131–140			10	0				
141–150			10	0				
Control...	12	2	10	0	10	0	10	0
Control...	15	2	10	0				

* Trials 71–80 for Bentia followed the first control series.

On October 2 Bentia was given a regular series in which she made no mistakes. About an hour later she was returned to the apparatus for a control series, but again she was emotionally disturbed, screamed and rushed about the apparatus. The experiment was interrupted and resumed after she had somewhat quieted down, but again she made two errors. Both of these controls are considered invalid because of unfavorable conditions. In each the subject was required to choose until she entered the correct box. The excuse for conduct of the experiment under conditions which were immediately recognized as unfavorable is that I was compelled to discontinue work after October 2.

The controls for Soda and Al were given under favorable conditions and provided convincing evidence of perfect adaptation. Because of limitation of my time it was necessary to give Mamo her control series, if any were to be given, on the day on which she solved the problem, October 2. This irregularity undoubtedly was unfortunate; nevertheless Mamo's performance was excellent. In the first trial of the series she was diverted by a moving and brilliantly illuminated area toward the right end of the response compartment and made what was quite obviously a careless mistake. This setting, when repeated at the end of the series, yielded correct response and I therefore recorded the series as perfect.

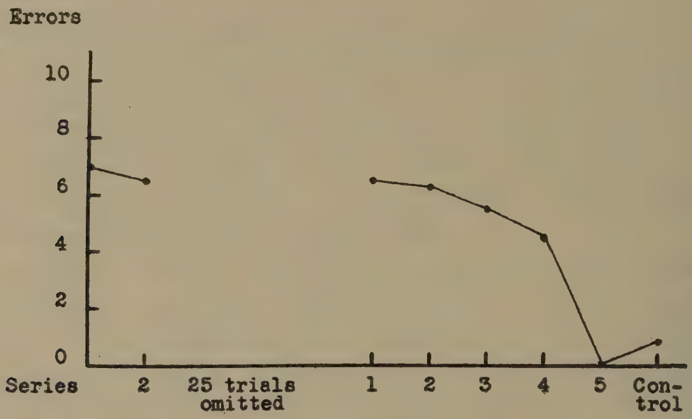

FIG. 8. ERROR CURVE FOR FOUR CHIMPANZEES IN PROBLEM 6, THE SAME BOX, 5, IN ALL GROUPS

The relative difficulty of the boxes varied extremely for the different individuals, table 30. The end boxes, 1 and 9, were very difficult for Bentia, Soda, and Al, whereas they were much less difficult than intermediate boxes for Mamo. The settings, table 31, with the exception of no. 7 (boxes 5 and 6), did not differ pronouncedly in value for the several subjects, but as it happened, setting 7 proved very easy for Bentia and Mamo, who indeed made no mistakes on it, whereas for Soda and Al it was approximately as difficult as any of the others. Observation of the behavior of the subjects during the trials gave me the impression that the larger groups usually were decidedly more difficult than the smaller, and although this impression is sustained by the results of table 32, the indicated differences in difficulty are much less than I should have expected.

TABLE 30

Relative difficulty of boxes (1–9) in problem 6

SUBJECTS	BOXES								
	1	2	3	4	5	6	7	8	9
Average number of incorrect responses per box for all settings									
Bentia	.358	.429	.095	.036	.000	.143	.200	.179	.381
Soda	.786	.500	.179	.134	.000	.161	.157	.286	.881
Al	.429	.464	.238	.268	.000	.375	.114	.357	.619
Mamo	.150	.425	.250	.425	.000	.363	.240	.500	.267
Average	.431	.455	.191	.216	.000	.261	.178	.331	.537
Order of increasing difficulty of boxes (by number) for the ten settings combined									
Bentia	4	3	6	8	0	7	1	9	2
Soda	4	7	6	3	0	8	2	1	9
Al	7	3	4	8	0	6	1	2	9
Mamo	1	7	3	9	0	6	2 =	4	8
Combined order	7	3 =	4	6	0	1	8	2 =	9

Soda, in review presentation of problem 6, after a rest interval of approximately nine weeks, instead of choosing box 5 immediately and regularly on the basis of her previous experience, reverted to her earlier habits of choosing end boxes. Sometimes

TABLE 31

Relative difficulty of settings in problem 6

SUBJECTS	SETTINGS									
	1 1–6	2 3–9	3 4–6	4 5–9	5 2–7	6 4–5	7 5–6	8 2–8	9 3–5	10 1–9
Number of trials per setting prior to disappearance of errors										
Bentia	6	4	4	5	6	3	0	6	3	4
Soda	11	13	12	13	13	12	10	13	13	13
Al	4	4	5	6	6	6	5	4	4	6
Mamo	9	9	7	8	8	9	0	9	9	8
Average	7.5	7.5	7.0	8.0	8.3	7.5	3.8	8.0	7.3	7.8
Total number of responses per setting prior to disappearance of errors										
Bentia	13	7	5	10	14	4	0	23	4	12
Soda	24	48	15	31	29	13	15	36	16	58
Al	15	17	20	14	16	10	8	18	8	16
Mamo	31	27	20	14	27	16	0	23	17	39
Average	20.8	24.8	15.0	17.3	21.5	10.8	5.8	25.0	11.3	31.3
Number of correct first responses per setting to and including first perfect series										
Bentia	2	5	6	4	2	6	7	1	6	3
Soda	5	1	12	1	4	13	9	2	12	1
Al	3	3	3	1	2	3	4	3	4	2
Mamo	3	4	5	6	6	3	10	5	2	4
Average	3.3	3.3	6.5	3.0	3.5	6.3	7.5	2.8	6.0	2.5
Order of increasing difficulty of settings (by number) as derived from above data										
Bentia	7	6 =	9	3	2	10	4	1	5	8
Soda	6	3 =	7	9	1	5	4 =	8	2	10
Al	9	7	1	2	6 =	8	3	4 =	5 =	10
Mamo	7	4	3	5	8	6	2 =	10	9	1
Combined order	7	6	3 =	9	4	2	1	5 =	8	10
Number of correct first responses per setting without interruption to and including first perfect series										
Bentia	1	3	3	2	1	4	7	1	4	3
Soda	3	1	2	1	1	2	4	1	1	1
Al	3	3	2	1	1	1	2	3	3	1
Mamo	1	1	3	2	2	1	10	1	1	2
Average	2.0	2.0	2.5	1.5	1.3	2.0	5.8	1.5	2.3	1.8

TABLE 32

Relative difficulty of size-groups of box settings for problem 6 as indicated by number of trials and successes

SUBJECT	NUMBER OF BOXES IN SETTING					
	2 (2 settings)	3 (2 settings)	5 (1 setting)	6 (2 settings)	7 (2 settings)	9 (1 setting)
Number of trials for solution (disappearance of errors)						
Bentia	1.5	3.5	5.0	6.0	5.0	4.0
Soda	11.0	12.5	13.0	12.0	13.0	13.0
Al	5.5	4.5	6.0	5.0	4.0	6.0
Mamo	4.5	8.0	8.0	8.5	9.0	8.0
Average	5.6	7.1	8.0	7.9	7.8	7.8
Number of correct first responses per setting to and including first perfect series						
Bentia	6.5	6.0	4.0	2.0	3.0	3.0
Soda	11.0	12.0	1.0	4.5	1.5	1.0
Al	3.5	3.5	1.0	2.5	3.0	2.0
Mamo	6.5	3.5	6.0	4.5	4.5	4.0
Average	6.9	6.3	3.0	3.4	3.0	2.5

it was the left end, and again the right. Only one of her five incorrect responses, prior to re-solution of the problem, was made on other than an end box. The response and error results follow:

TRIALS	RESPONSES	ERRORS	TRIALS	RESPONSES	ERRORS
1–10	15	4	31–40	10	0
11–20	11	1	Control	10	0
21–30	10	0	Control	10	0

Inasmuch as there was no way in which Soda, in advance of actual trial, could know what was demanded of her in the experiment, it is not surprising that she made four errors in the initial series. The following day she made but one error, and the next day, and the next, her responses were perfect. There followed on successive days two control series, in which the subject responded correctly with ease and assurance. It may not fairly be said that Soda had forgotten her acquired adaptation to the problem 6 situation; instead she remembered the inappropriate acquired response, namely, that for problem 1 or that for problem 3. The promptness with which she adjusted to the immediate situation and responded correctly is evidence of the retention of her previous discovery of the cue to adaptive response to problem 6.

RETENTION AND RE-ADAPTATION

Obviously, measurements of retention or persistence of effects of multiple-choice experience cannot be made to advantage if between original training and retesting the subject is presented with a new multiple-choice problem. Even when this is not the case, an animal which has been used in two or more relational problems, whether or not successfully, is sure to exhibit conflicts and competition of reactive tendencies which affect the results of review, retesting, and relearning. In a word, conditions could scarcely have been more unfavorable for measurement of retention than in this particular investigation. Under the circumstances, it would be unreasonable to expect adaptation to a given problem to be perfectly retained. Yet, one might anticipate speedy reacquisition on re-presentation. The results obtained in the few retention experiments which I made in many respects are illuminating. Although previously referred to under appropriate problem and subject, they will be reviewed summarily at this point.

Mamo, who in 1932 solved problem 2 (second from right end), failed when it was re-presented after approximately eight months. She had lost the solution and within one hundred re-training trials she made no better error showing than did her three companions who had not succeeded in solving the problem during 1932. That she obtained high scores occasionally and succeeded in adapting to the problem when it was presented in such easy forms as uniform 1–4 setting, or settings limited to four boxes, suggest her near approach to perfect adaptation. Always for her, both in the season of 1932 and in that of 1933, solution appeared to be slightly beyond her capacity. My only explanation for her failure to re-adapt is the over-difficulty of the problem. It should not be overlooked, however, that experience in problem 3, the right-end box, supervened between Mamo's original work on problem 2 and its re-presentation.

Yet another case with Mamo. For her, problem 3, the right-end box, when originally presented seemed fairly easy of solution. But when it was re-presented to her in the season of 1933 following the re-presentation of problem 2, she not only failed to respond correctly at first, but even within the limits of the original training, 170 trials. The interval between training and retesting was about eight months, but in all probability the re-presentation of problem 2 was much more largely responsible for disturbance of retention and prevention of ready re-solution than was the rest interval. I suspect indeed that work on problem 2 was peculiarly disturbing to the subject because of its extreme difficulty and consequent persistent failure. It does not seem at all strange to me that Mamo should have lost her adaptation, but I find it difficult to understand why she did not re-achieve it promptly.

The only instance of an uncomplicated test of retention is supplied by Soda. In July, 1933, she successfully solved problem 6. Thereafter, until given a retention test approximately nine weeks later, she was not used in the multiple-choice apparatus. Presumably, then, she might be expected to respond correctly on re-presentation of the problem. Actually in her first retention series she made four initial errors: one second from the left choice, two left-end choices, and one right-end choice. In her next daily series the only error was a left-end choice. Clearly, end-box habits initially dominated over subsequently acquired reactive tendencies and as a result Soda made four errors in her first and exploratory series. She did not wholly escape the influence of her end-box reaction tendency until the third series, which was perfect.

Together these three attempts to test retention and re-adaptation demonstrate the great importance of amount and duration of work on a problem, whether or not it be solved, and of the competition and conflict of reactive tendencies, by contrast with the relatively slight significance of recency of training. The last problem to be solved is not necessarily the one which asserts its influence on re-presentation of the situation.

It is excusable to emphasize the unusual circumstance that the subject, unless each problem has a distinctive symbol, such for example as the black board used in problem 4 or the white board of problem 5, can tell only by preliminary trial whether an old or a new problem is being presented by the experimenter, and if an old problem, which. This fact should not, however, militate against the subject's use of the most recently acquired mode of response. It appears that previously acquired adaptive reactions tend to reappear in the reverse order of acquisition.

From the varied aspects of the results of this inquiry it may confidently be inferred that numerous acquired tendencies and patterns of response are retained from month to month and some from season to season, but that in the solution of relational problems in the multiple-choice situation such acquisitions are likely to prove disadvantageous. Memory, from this point of view, may be said to play a minor rôle in the achievement of adaptations.

MOTIVATIONAL FACTORS AND CONDITIONS

Endeavor was made throughout the investigation to discover and to maintain optimal conditions, motivational and otherwise, for adaptation to the multiple-choice situation and for problem solution. Evaluation of motivational factors was not a primary objective, since the conditions of work were generally unfavorable to reliable measurement. Varied behavioral evidences support the inference that the motivation of the subjects usually was highly favorable, that it rarely was too weak, and that occasionally it may have been over-strong. Frequently it was indicated that too great eagerness for success in the experiment was even less favorable to problem solution than transient carelessness or indifference.

In review, it may be stated that both positive and negative motivational factors were employed in various stages of the inquiry and in numerous combinations. This was done with intent to discover optimal conditions. Chiefly important of the positive factors were food and the results of coöperation with the experimenter, among which doubtless the satisfactions of completion of the day's work and return to cage companions are most deserving of mention. Among negative conditions appear: (*a*) closing of entrance door of incorrectly chosen box, either with or without locking; (*b*) confinement in incorrectly chosen box for five to a maximum of sixty seconds; (*c*) electric shock as punishment for incorrect response; (*d*) deprivation of reward or lessening of the amount of food for trial unless initial response was correct; (*e*) vocal signal of failure, which when given by the experimenter seemed to be accepted as a reprimand; (*f*) prolonged blast on police whistle, likewise as signal of failure; (*g*) closing of entrance door to incorrectly chosen box with a bang to indicate mistake.

Positive factors, it was thought, might tend to confirm and reënforce correct response; negative factors, to discourage and inhibit incorrect response. But in the light of the results of the inquiry, it is doubtful whether either type of condition did more than provide opportunity for discovery of the essential feature of the problematic situation. The conclusion is suggested that so long as the chimpanzee subject was interested in its task and would continue to work for escape by completion of the circuit through the apparatus, particular reënforcing or inhibiting factors were of relatively little value, for the obvious reason that they served neither to eliminate incorrect modes of response nor to encourage correct modes. This was the case obviously because a particular response which was correct for one setting might be incorrect in the next setting, and in consequence, reënforcing and inhibiting factors tended to cancel one another. By contrast with the effect of particular motivational conditions, change in conditions appeared to be preëminently effective in bringing about modifications of behavior and new patterns of response. Thus, often, a subject was enabled to discover the solution of a problem.

Initially it was my expectation that a certain constant combination of motivational factors would prove most favorable to success, but observation clearly enough indicated that I was mistaken. Conditions which are unfavorable to initial general adaptation may be entirely suitable later. Hence the desirability of change of conditions and of their graduation in accordance with the status of the subject in the experiment and the nature and results of its previous experience and approaches to success.

Relative to the significance of positive rewards, the investigation demonstrated the extreme importance of social factors. Initially, companionship was used by the introduction of the subjects to the apparatus in pairs. This effectively promoted general adaptation. The individuals stimulated one another to activity and effort; thus their responses to the settings of the apparatus were facilitated without obvious imitation. Later, when the subjects were used alone, companionship undoubtedly persisted as condition, inasmuch as it was immediately achieved on completion of the day's work. Presumably it was one of the animals' chief incentives for coöperation with the investigator and continuation of effort until completion of the series of trials. It is noteworthy that throughout the series of problems the coöperation of the several subjects with the experimenter was almost perfect. Undoubtedly this is attributable in considerable measure to the regularity of work, for the subjects were used every day, with few exceptions, and except at the beginning of problems the length of a period of effort in the apparatus was measured by ten trials. They came finally to accept precisely this and nothing more. Often it was obvious that they anticipated the end of the series, and quite commonly they objected if, as sometimes happened, additional work was expected of them on completion of the regular series. In no case did a subject refuse to complete its series of trials except in the event of such unusual circumstance as disturbing external conditions or extreme overstimulation. An example of the former is the sound of a cement mixer, which one morning completely interrupted the investigation; undoubtedly the explosions of the engine were alarming.

The application of inhibiting factors exhibited several interesting phenomena and relations thereof, and provided the basis for generalizations such as the following. Manifestly, a type and degree of punishment for mistakes, which early in the period of work would completely upset a subject, could subsequently be used to advantage. This was demonstrated alike for period of confinement in boxes, for electrical stimulation, and for the withholding of food or the presentation of relatively disliked food. Furthermore, and this appears to be of the utmost practical and theoretical importance, the results of this investigation show that the more difficult, baffling, and confusing a given problem or task, the greater the disturbing effect of an unusual stimulus or circumstance. This is illustrated by such examples as the following. A subject which is responding with reasonable ease and degree of success in the multiple-choice situation will pay relatively little attention to the presence of a visiting observer or to an unusual noise or sudden shower; whereas the same unusual circumstance, if the animal is working with difficulty and without success in the multiple-choice apparatus, almost invariably induces pronounced response. Clearly the greater the emotional tension of the subject, the more likely and the more marked its response to a distracting, interrupting, or annoying stimulus or situation. A corollary to the above is the practical deduction that the more difficult the task which the chimpanzee is required to perform, the weaker should be the negative or inhibitory motivational factors. I have formulated thus crudely what appears to be a law of distractability. Whether it applies to other situations than that presented in this investigation and to other organisms than chimpanzee I am not prepared to hazard an opinion.

A peculiarity of response to negative motivational conditions which I have not observed in the behavior of other organisms was exhibited by the chimpanzee subjects of this investigation. It may be described as delayed effect of over-stimulation. The facts may be stated thus. On a given day a subject might respond without evidence of disturbance to a certain frequency and duration of confinement in boxes or to a certain strength and frequency of application of electrical stimulation, and the investigator, as a result of his observations, might conclude that the punishment or stimulus conditions were satisfactory. The following day, however, the subject would respond to identical punishment with extreme disturbance of behavior, including, often, pronounced slowing of response, inhibition of certain types of response, or even complete refusal to work. The interpretation of these facts is difficult. My suggestion is that initially, and on the first day, the subject accepts the conditions as an essential part of the total situation and somewhat as a matter of course, primarily because of its perfect adaptation to the experiment and its long-exercised habit of coöperating with the experimenter. On the following day, or subsequently, the condition of the subject differs in that it anticipates the unusually disagreeable or exasperating conditions to which it was previously subjected, and the effect of the conditions thus is so far enhanced that there is a complete breakdown emotionally, if not also in adaptive response. Repeatedly in the latter half of this investigation, I was misled in my judgments about the suitability of punishment by the initial behavior of the subjects. Several times over-stimulation occurred with resulting interference with work for a number of days.

From observations in this investigation it may be stated that given a moderately strong drive or lure, the subjects appear to work best when attention is not monopolized by an unfamiliar compelling stimulus. Neither large and especially desired rewards nor obviously severe punishment favor adaptation to the multiple-choice situation through discovery of its essential feature. Instead, mobile attention, confidence in the experimenter and the apparatus, thorough familiarity with a routine procedure, freedom from well-established habits of response to particular settings and from automatisms, stand out as particularly significant desiderata. My chief practical conclusion is that it is essential to command the interest and favorable attitude of the subject and wholly undesirable to use especially strong positive or negative motivational conditions. This I suspect is true because the affective status of the subject is very much more important as condition of problem solution than is mere strength of reënforcing or inhibiting factors.

AFFECTIVE AND ADAPTIVE STATUS

Daily observation of effort and degree of adaptation to the problematic situation, and the statistical data as well, indicate that affective stability resulting from familiarity with the situation, self-reliance, poise, and calm interest in the task of adaptation were far more important as conditions of discovery and resultant success in the experiment than was degree of behavioral adaptiveness or docility, as gauged by the performance of a subject in this experiment and by its behavior in various other types of experiment. This is somewhat surprising, for one might naturally assume that adaptiveness would be supremely important. Yet Mamo, my most successful subject in the first season of work, happened also to be the youngest, the most dependent socially, the most infantile in behavior, and as indicated by certain other experiments, also the slowest in behavioral adaptation. Nevertheless, she alone solved problems 1, 2, and 3 during the first season, whereas her companions solved only problem 1.

Emotional conditions and disturbances, such as are suggested by the subjective terms timidity, fear, resentment, anger, apprehension, manifestly are unfavorable to the solution of multiple-choice problems.[5] Consequently, perfect general adaptation and familiarity with the total situation are indispensable to efficiency of work and condition success. Had I not been experienced in the use of various types of primate in the multiple-choice situation, I suspect that I should have lost many days by reason of breakdowns of adaptation and failure of coöperation. Probably I should have induced neuroses which, in addition to wasting time, would have complicated the internal conditions of response and prevented adaptation. Actually I did my utmost to avoid such undesirable developments, while attempting to command the perfect coöperation of my subjects. Only twice during the investigation did they become refractory and threaten to quit work. In both of these instances inhibition clearly resulted from over-stimulation electrically or over-long and too frequent confinement in incorrectly chosen boxes. The almost complete avoidance of transient neuroses is notable, in view of the experience of investigators in comparable situations, where adaptation is either impossible or extremely difficult for the subject.

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[5] Such subjective terms as appear herein, applying to chimpanzee, refer not to the experience of the subject, but to the behavioral picture which is implied in the term. Given unlimited space for description or adequate materials for pictorial representation, the observed behavior might be so nearly adequately described as to obviate the need of subjective terminology with its appearance of anthropomorphism. Actually neither subjectivism nor anthropomorphism is intended, or from the point of view of the writer allowable. For it is simply and solely a matter of brevity of statement and of necessity either of using altogether familiar subjective terms or of inventing new terms for the designation of behavioral patterns or pictures.

If the principal observations and most obvious indications of this investigation are reliable, a very considerable portion of our experimental work on infrahuman organisms is rendered of little value, if not positively misleading, by reason of failure to take affective conditions into account and either to standardize and control them or to make adequate descriptive measurements. Something of what I have in mind as applicable particularly in the study of primates is suggested by the assertion that the organic conditions designated by optimism, hopefulness, expectation, or anticipation of success are of extreme importance in the relation of chimpanzee to relational problems. The logical inference is that to attempt to measure behavioral adaptation while neglecting its affective conditions is sheer waste.

Throughout this inquiry the experimenter obviously was an important feature of the situation, for although he observed from behind the subject and was partially screened from it, he was always in a measure visible if it desired to see him. As a matter of course, the subjects at various times sought to obtain cues to correct response by watching me. Sometimes this was done persistently throughout a series of trials, and even on successive days. To the experimenter the direction of the animal's attention was always obvious, because it had to turn toward him in order to observe. Always, but especially at such times of concentrated interest on the part of the subject, I tried to avoid giving reliable cues. My notes show that the animals as a rule soon became discouraged in their efforts to obtain help from me and ceased to try. Doubtless this was because I was on the alert at such times, and more often than not by direction of gaze and limb or body movements misled them. This, indeed, was intentional on my part in order that they should be promptly discouraged in their search for extraneous cues.

The experimental data abundantly prove that secondary cues, whether from observer or elsewhere, did not serve for problem solution. Among the control tests and checks which were used appear: complete change in the procedure of setting the boxes and releasing the subject for a trial; replacement of the observer by another, and to the subject unfamiliar, experimenter; the use of head covering and smoked glasses by the observer to prevent the subject from noting direction of gaze or eye movement.[6]

PREDICTABILITY OF PROBLEM SOLUTION

Students of animal behavior ordinarily expect, after long acquaintance with a given type of animal or individual, to be able to predict with reasonable certainty the fact, nature, course, and speed of its adaptation to a definite experimentally arranged situation. In the last thirty years I have worked with many and widely diverse types of organism in many kinds of experiment which required either general or specific adaptations, and never, until I began to study primates in the multiple-choice situation, have I found myself lacking useful observational basis for prediction concerning adaptation. At the beginning of the investigation here reported I fully expected to discover eventually characteristics of chimpanzee response which would enable me to say either that the animal would solve a certain problem or would not. At the conclusion of the task I admit that I am unable to do so. Despite prolonged intensive observation, during which my anthropoid subjects undoubtedly worked at least as hard as I did, I find myself wholly without ability to predict the outcome of a given individual's work in such multiple-choice problems as were used in this investigation. All that I can do is to guess as to the essential features of adaptive effort; the results of such effort are entirely problematical.

[6] It was not by oversight that the observer was included in the situation. Experience in working with chimpanzee has taught that in many kinds of experiment it is desirable to command coöperation by contact, visually at least, between S and O. Either way there are advantages and disadvantages, and for a given type of experiment choice is primarily a matter of practical judgment and of intent. In this case it was my practical judgment that I might better function as a part of the experimental situation than eliminate myself from it during the reactions of my subjects.

It may reasonably be inferred from the results and generalizations which have already been presented that some of the problems given to my chimpanzee subjects were near, or actually beyond, the limits of their capacity for successful adaptation, and for this reason, among others, proved peculiarly difficult. This statement certainly is not applicable to problems 1, 3, and 6, which were solved by each of the four subjects. Nevertheless, during their work on these soluble problems I found it unexpectedly difficult to predict the progress of improvement, the fact or the time of solution of a problem, or even the order in which the several subjects would finish the task.

Under the heading, Basis of prediction of success in adaptation, one may consider: (*a*) the general or total behavior of the organism in the apparatus day by day; (*b*) the response and error data for successive series of trials; (*c*) methods or patterns of response to specific settings and series of settings, and (*d*) the affective and attentional characteristics and status of the subject. In turn I shall comment briefly on the values of these several bases of predictive judgment.

On the assumption that I should soon learn what to expect of my subjects by careful observation of their general behavior, I systematically endeavored to anticipate from day to day the results of the next series of trials. So uncertain was my forecast that I finally had to admit my inability to discover indications of approaching success in the general behavior of the subjects.

Statistical data of response, error, and time also proved next to valueless in all difficult problems. Generally, marked diminution in errors and in time of response led me to anticipate problem solution; yet as often as not success came without such change in statistical values, suddenly, and to my complete surprise. From among many available and similar illustrations I cite the following in support of this generalization. I have selected intentionally an easy problem, because if anywhere one should expect to find there relatively clear evidences of approaching success. This is the illustration. In the midst of the work of the four chimpanzees on problem 6 (same box) Doctor Kenneth W. Spence, on September 29, 1933, as visitor, observed each of my subjects throughout its regular series of trials. Experienced in the experimental use of young chimpanzees, the visitor was well qualified to judge from what he observed concerning the probable course of adaptation. Therefore at the end of the day's work I asked him to state his expectation. It was as follows: that Mamo almost certainly would finish in the following series, September 30; that Bentia might, but probably would not, finish in the next series; that Al certainly would not finish as soon as the other two. Soda had previously solved the problem. Actually this appeared from later results: both Al and Bentia solved the problem in their next series, September 30, whereas Mamo did very poorly indeed.

In this particular practical situation, and when asking the judgment of Doctor Spence, I admitted my utter inability to foresee the course of events, although I had then worked with my subjects almost daily for twelve months, and in many instances could anticipate their specific responses to a particular setting, their mannerisms, and their attitudes toward various features of the situation. Doctor Spence was surprised by what happened, whereas I had passed beyond the possibility of surprise.

Even when errors in initial response dropped to ten per cent it proved unsafe to count on problem solution quickly, or even eventually, for often the cue on which the subject relied was lost or turned out to be inadequate. Review of the data for series errors in tables 5, p. 18; 10, p. 30; 15, p. 40; 16, p. 45; and 25, p. 69, discovers more instances in which a single error, that is ten per cent failure in a series, was followed by increase in number of errors than by disappearance of errors and problem solution.

Specific aspects of behavior, and especially methods or modes of response to the situation, proved somewhat more useful and often I was able to presage improvement or even problem solution on this basis alone; but again, and more frequently than not, I failed. Especially when a subject suddenly changed its mode of response, began to hesitate before open boxes and to go from one to another as if searching for something, I was strongly tempted to expect problem solution. Occasionally it came promptly. An example is supplied by Soda in her initial solution of problem 6. During a number of series she had responded fairly directly and immediately by selecting a box and dashing into it. There was little evidence of choice after she entered the response compartment. Quite without warning, at the beginning of the 14th series, she inhibited her dash toward an open box, turned instead sharply to her right, and for several seconds delayed in the food receptacle corner of the response chamber. Usually throughout the period of delay her attention was fixed on the open doors and it seemed as though she were attempting to select from among them. When she approached them, instead of dashing into one instantly, as if by previous decision, she often hesitated and walked back and forth before the open doors. Never, after she abandoned her direct and dashing method of choice for the more deliberately selective procedure, did she make a mistake. Many other examples of the significance of method or mode of response and of its predictive value might be given, but all point in the same direction, although few as definitely as does the illustration.

There was a time, and it persisted for weeks, when I thought that I could depend on the behaviorally expressed anticipation and affective attitude of my subject to warn me of the near approach of success. The facts are as follows. From time to time, but not very frequently, a subject seemed exceptionally eager to get to the apparatus for its day's work. At such times it often made me feel that it was actually hopeful of success and had a presentiment that it at last could meet the baffling situation adequately. This type of evidence also proved utterly unreliable. The subjects seemed as liable to be misled by their internal or external indicators as was I by those which I attempted to use.

In table 33 have been assembled, for convenience of consultation, for each subject and problem, the total number of trials given, exclusive of control series, the number of errors in the last five regular series, the number of errors in the control series, and the classification of result as solution by approximation, sudden solution, or failure.

From this table the following statistics of problem solution are derived: Number of cases of presentation of problems, 24 (6 problems for each of 4 chimpanzees); number of problem solu-

TABLE 33

Summary of results (errors) in final series for all problems and subjects

SUBJECTS	TOTAL REGULAR TRIALS	ERRORS IN LAST FIVE SERIES	ERRORS IN CONTROL SERIES	CLASSIFICATION OF SOLUTION
Problem 1, left-end box				
Bentia	410	3, 5, 1, 2, 0	0	By approximation
Soda	180	5, 6, 5, 2, 0	0, 0	By approximation
Al	190	5, 5, 3, 2, 0	0, 0	By approximation
Mamo	300	3, 1, 2, 1, 0	0	By approximation
Problem 2, second from right end				
Bentia	1000	Only 90% correct		Failure
Soda	1130	Only 80% correct		Failure
Al	1110	Only 90% correct		Failure
Mamo	170	5, 6, 5, 5, 0	6	Sudden
Mamo (2d solution)	380	2, 2, 3, 0, 0	2, 2	Sudden
Mamo (review)	240	Only 90% correct	2	Failure
Problem 3, right-end box				
Bentia	150	1, 2, 1, 0, 1	0, 1	By approximation
Soda	130	5, 2, 2, 0, 0	0, 0	By approximation
Al	160	5, 3, 1, 1, 1	0, 1	By approximation
Mamo	170	3, 2, 2, 0, 0	0, 0	By approximation
Mamo (review)	170	Only 80% correct	3, 4	Failure
Problem 4, middle box				
Bentia	400	6, 6, 7, 8, 7		Failure
Soda	400	5, 5, 7, 6, 5		Failure
Al	400	5, 6, 6, 7, 5		Failure
Mamo	400	3, 4, 9, 9, 8		Failure
Problem 5, alternately left end and right end				
Bentia	600	Only 80% correct		Failure
Soda	400	3, 3, 0, 1, 0	2, 0	Sudden
Al	600	Only 80% correct		Failure
Mamo	600	Only 90% correct		Failure
Problem 6, same box (5)				
Bentia	80	5, 3, 3, 0, 0	2, 2*	Sudden
Soda	150	6, 7, 6, 0, 0	0, 0	Sudden
Soda (review)	40	4, 1, 0, 0	0, 0	Sudden†
Al	70	7, 8, 6, 4, 0	0	Sudden
Mamo	100	4, 6, 6, 5, 0	0	Sudden

* On the day following her first control series Bentia was given first a regular series in which she was perfect and thereupon a control series in which she made two errors.

† Classified as "sudden" because only two series of trials were required for solution.

tions,[7] 14 (58 per cent); number of instances in which solution followed a series with three or more errors, 6 (43 per cent). Of all problem solutions approximately one-half were abrupt or sudden; of the remainder some may represent sudden discovery of the essential relationship, followed by failure to achieve solution immediately because of the interference of some acquired reactive tendency. Evidence of discovery, either with or without problem solution eventually, appears in the response and error data for Bentia and Mamo in problem 1 (table 5, p. 18), for Bentia and Soda in problem 2 (tables 10 and 15, pp. 30, 40), for Al in problem 3 (table 16, p. 45), and for Mamo in problem 5 (table 25, p. 69).

No solutions were achieved clearly by adaptation to specific settings and to the particular order of settings. Had such been the case the control series should have upset the adaptation and evoked numerous incorrect responses. Presumably had a given setting been independently mastered, errors would not have recurred after periods of success. Some settings proved much easier than others; a few were adapted to perfectly.

On the completion of observations I attempted to predict from response and error data the order of diminishing success of the four subjects in each problem. For problem 1, prediction was based on the errors in series 1–16, and the final rating on the number of trials required for success. For problem 2, prediction was based on the errors in the series 1–50, with due regard to Mamo's initial and early success, and the outcome of the experiment was judged by the order of approach to success at the end of the training. For problem 3, prediction was based on the errors for series 1–10, and the outcome on the trials required for solution of problem. For problem 4, prediction was based on the errors for series 1–20, and since no one of the subjects solved the problem, actual achievement was based on their approach to solution as indicated by statistical data. For problem 5, prediction was based on the errors for series 1–30, and solution on Soda's success and the approach of the others to a perfect score.

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[7] Solutions on re-presentation are omitted, and Mamo's dual solution of problem 2 is counted as one.

For problem 6, prediction was based on errors for series 1–6, and the outcome on the order of success.

Below are presented for each of the six problems the observer's expectation, and beneath it the actual outcome of the experiment.

Problem 1.	Mamo	Bentia	Soda	Al	Expected
	Soda	Al	Mamo	Bentia	Realized
	Displacement 8 points				
Problem 2.	Mamo	Soda	Bentia	Al	Expected
	Mamo	Al	Bentia	Soda	Realized
	Displacement 4 points				
Problem 3.	Soda	Mamo	Al	Bentia	Expected
	Soda	Bentia	Mamo	Al	Realized
	Displacement 4 points				
Problem 4.	Soda	Mamo	Al	Bentia	Expected
	Soda	Al	Bentia	Mamo	Realized
	Displacement 4 points				
Problem 5.	Soda	Bentia	Mamo	Al	Expected
	Soda	Mamo	Bentia	Al	Realized
	Displacement 2 points				
Problem 6.	Bentia	Al and	Mamo	Soda	Expected
	Bentia	and Al	Mamo	Soda	Realized
	Displacement 1 point				

Finally, my practical judgment, as based upon all available general observational and statistical evidences, proved reasonably reliable only when there happened to appear in conjunction a number of signs to which one ordinarily would attach positive values. For example, small percentage of errors, careful selection of box to be entered, optimistic attitude or hopefulness, obvious attention to the settings as indicated by direction and continuity of gaze. There were instances, however, in which even with such a constellation of favorable signs, success did not appear.

In the end, somewhat chagrined by my failures, for in a lifetime of behavioral work one expects to achieve both inclusiveness and keenness of observation and insight, I was forced to admit inability to predict the success of my chimpanzee subjects in relational problems. Possibly my failure resulted rather from conflicts among problems than from their distinctive characteristics, for it cannot be doubted that everything would have been very different indeed if I had been able, at the end of work on a given problem, to eradicate completely its effects and to start fresh on a new task. Instead, reactive tendencies, modes of response, anticipatory responses persisted, and general adaptations became increasingly numerous and complicated in their relations with the progress of the investigation, until finally even the simplest multiple-choice problem (such as the same box, as in the 1–4 setting) was difficult and baffling to the animals instead of readily soluble. By their long-continued and discouraging experiences, these chimpanzees had become blinded to aspects of the situation which otherwise would have been conspicuous and rarely would have been overlooked. Habits which in the main proved unfavorable to problem solution increasingly replaced naïve adaptivity and customary open-mindedness!

PRINCIPLES OF ADAPTATION (PROBLEM SOLUTION)

Direction, distribution, and concentration of attention are exhibited by this investigation as primary conditions of problem solution and perfection of adaptation. Progressively the habitual occupation of attention with irrelevant aspects of the experimental situation served to delay or to prevent discovery of its essential feature. The more the subject tended to become automatized in the experiment, the less likely became problem solution. Attention, it would seem, must be mobile, fluctuating, and all-embracing, yet also capable of fixation once the essential relation is happened upon, and identified with satisfaction.

It is demonstrated by this investigation that the acquisition of reactive tendencies does not necessarily favor the appearance of functional patterns of response of which the simpler processes are essential parts. Instead they may, and in many instances obviously do, lead to conflicts which prevent or delay adaptation. It seems then that for the solution of multiple-choice problems naiveté may be more favorable than experience with similar situations. Automatisms are especially prejudicial to the discovery of relations. The subject seems to be enslaved by its acquisitions. Habit therefore, herein, appears as foe of progress through discovery.

Abruptness of behavioral change is characteristic of chimpanzee. Sudden alterations appear in affective attitude, direction and distribution of attention or interest, response to features of the apparatus and observer, as well as in adaptation. Problem solution between series or over-night, in view of this essential fact, might be expected.

Ordinarily, behavioral adaptation of chimpanzee to relational problems is not achieved by gradual process of approximation, as for example in the maze situation and in many forms of sensory discrimination experiment, but instead by a sudden discovery which in itself suffices to complete and perfect adaptation almost instantly. "Learning," as biological process, may consist in the reënforcement of positively toned acts and the inhibition of negatively toned, until finally by the selectional process, which through Jennings and Thorndike has come to be termed "trial and error," more or less adequate patterns of behavior have been acquired. But discovery, by contrast, and as herein defined and used, may or may not appear as contributory to success. In many animal experiments, discoveries doubtless are made which direct, limit, and facilitate the selection and integration of acts or the confirmation of a given simple form of response. Their importance varies extremely. It happens that in multiple-choice problems, success may result from a simple discovery. It therefore is all-important.

I would maintain hypothetically, as a result of my study of chimpanzee adaptation, (1) that discovery is not necessarily present in "learning" and (2) that solution of relational problems such as those herein described usually is not achieved by chimpanzee without it. The evidence in my opinion supports the contention that discovery often comes abruptly, without warning of any sort thus far detected, and that even in those instances in which the gradual elimination of errors makes it appear that the process was gradual, critical examination of the observational data indicates that, although sudden discovery occurred, perfect adaptation was not immediately achieved because of some conflicting process. In many instances, a subject, disturbed in the midst of or on the threshold of discovery, loses or abandons its cue and reverts to inadequate modes of response. This observation is extremely interesting and significant. It supports my conclusion that affective attitude is highly important in connection with success in solving relational problems.

Of peculiar importance in our evaluation and interpretation of response of chimpanzee to multiple-choice problems is the success of my subjects in adapting to the requirements of the control settings. With few exceptions their solution of a problem transferred perfectly to the new settings and series. As a rule the subject responded with apparent ease, assurance, and satisfaction. Such behavior precludes the possibility of problem solution by acquired response to specific settings and order thereof. In none of the organisms (dove, crow, rat, pig, cat, Macacus monkey, orang-outan, man) whose efforts to solve multiple-choice problems I have had opportunity to observe, with the exception of man and possibly also orang-outan, has there appeared degree of ability to meet the control situation comparable with that of chimpanzee.[8] Herein, it would seem, is manifested superiority of anthropoid ape and of man over the other vertebrates. My present suspicion is that the contrasts exhibited by organic types depend upon the presence, or absence, and the nature of the act of discovery, which I believe marks the advent of "research" as mammalian activity, exercise, or profession!

In multiple-choice versus maze problems there is one versus many adaptations. The former requires a relatively simple behavioral adaptation, given capacity for the essential discovery, whereas the latter involves, or may involve, a very complex group or train of adaptations. Moreover, in many so-called learning or habit studies of animals (man is an animal!) there occurs something very like a wearing down of resistances and resultant facilitation of certain acts and patterns. By contrast, solution of a multiple-choice problem, as primary result of the discovery of a certain relationship (middleness, for example), may be a simple act which is reënforced, confirmed, and enhanced in affective value by the immediately appearing satisfactions of achievement. These, it must be understood, are much more than the obtaining of food, for it is manifest in the behavior of chimpanzee that achievement of success, after long discouraging and seemingly futile effort, is keenly appreciated by the subject. Indeed, being able to go through the apparatus promptly and without let or hindrance seems in the end to impress the subject even more favorably than the achievement of material reward or the avoidance of an anticipated penalty. The chimpanzee manifestly delights in the fact of success. Achievement appears then, within limits, to be its own reward and to be capable of inducing repetition. In this investigation it was supported by coöperation with the experimenter.

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[8] Doctor Kenneth W. Spence and I have undertaken a comparative study of the data on response to relational problems which have been made available by application of the box form of multiple-choice apparatus in studies of various birds and mammals. On this account no attempt has been made in this report to compare results for chimpanzee with those available for other mammals.

The laws of behavioral adaptation in the case of such multiple-choice problems as I have employed belong within the categories of attention, reënforcement, and inhibition. Precisely which principles within these important concepts are applicable and how they should be formulated in this connection remain to be discovered. Many of the factors or conditions which appear to be important in one or another type of learning or habit formation seem to be relatively unimportant or even non-existent in the chimpanzee's adaptation to this particular sort of situation. Frequency, recency, and effect are examples in point.

Learning is not a single, simple process, but instead multiple. In other words, there are types and varieties of behavioral adaptation. I predict that careful analytical study of accumulated observational data on habit formation in animals of various types and conditions will support this assertion.

"Trial and error" response, relational response, symbolic response, delayed response, anticipatory response—are they cases of learning or may they better be termed instead types of behavioral adaptation? It would seem that, like intelligence, instinct, and psychology, the term learning has lost its technical usefulness and sorely needs to be redefined and restricted in its application. Certainly not all cases of behavioral adaptation in animals possess the same characteristics or depend upon the same conditions.

SYSTEMATIZATIONS, METHODS, HYPOTHESES

Definite patterns of response, as for example, choice of boxes in order to the right or to the left, which persisted from day to day instead of merely during a daily series of trials, were rare in this investigation. Much more common were methods of response which appeared for a few trials and were then abandoned either permanently or temporarily. Often such methods recurred in the course of weeks of work on a problem. The following patterns were noted.

(1) Perseveration (repeated and successive choices of the same incorrect box). This was rare except when a subject faced a new problem or was disturbed emotionally by failure or punishment.

(2) Pronounced preference for boxes to the right of the middle of the apparatus. This probably resulted from the asymmetry of the apparatus. It differed markedly in the individual subjects and in the several problems.

(3) Persistence of the same mistake for a given setting in successive series and despite punishment designed to inhibit it. There are some extreme instances of such stereotypy in which the response appropriate for a previously presented problem would be given in almost every trial.

(4) Recurrence of a former mistake after several correct responses to a given setting. This type of irregularity was much more frequently exhibited by Mamo than by the other subjects.

(5) Tendency to eliminate in a given setting the boxes which had been correct in previous problems. Usually this occurred in the reverse order of problem presentation.

(6) Choice of the same box in all settings of the series in which

it happened to be available. This method of response was rare and appeared only in case of extreme bafflement or discouragement. It was exhibited notably by Al in problem 2.

(7) Tendency to choose a certain box, and in the event of mistake, to work systematically toward the right or the left of the starting point. Although this occasionally appeared, it seldom was long persisted in. Bentia exhibited it pronouncedly in setting 9 of problem 3.

(8) As method of response appeared the choice or selection of a given reaction mechanism, while the subject at door *x* awaited admission to compartment *B*. Contrasted with this method is that of entering *B*, turning in a given direction, and making selection of a box from a certain constant position.

(9) Passage to and fro before the group of open doors, with occasional halt to examine one, and final selection and entrance.

(10) The method or mannerism of turning about in a particular way, rolling into the boxes, or trying out various acts and modes of approach to the boxes, as though they might condition success. Such peculiarities and variations of behavior were numerous, highly individual, transient, and extremely difficult to interpret.

(11) Rushing into a box and out of it so quickly that the observer could not lower the entrance door. This happened rarely for other than incorrect choices, and it always made the observer feel that the animal was uncertain in its choice and, anticipating an error, thus attempted to escape its consequence.

In addition, there were many features of behavior which one naturally would think of as mannerisms, but which possibly may have been intimately related to adaptive effort. Illustrative of such acts are manner and direction of turning or of entering the boxes; closing of entrance door if it were not immediately lowered by the experimenter. Rarely did such activities or peculiarities of action obviously facilitate adaptation or problem solution; usually they impressed the observer as irrelevant, sometimes as transient mannerisms, again as playful antics, and now and then as experiments.

Under conditions of extreme discouragement temper tantrums were displayed by all of the subjects. Their appearance and frequency were inversely related to age. In Mamo they were most frequent and pronounced, with screaming, violent movements, sometimes rolling on the floor, with an occasional glance toward the observer to note whether he was moved to assist, for the behavior is as clearly utilitarian as in the human infant or child. Soda came next in liability to emotional disturbance and violent expression of the temper tantrum sort. Yet in the course of the investigation she only a few times responded to over-stimulation or over-strong punishment in this manner. Al and Bentia, the most resistant of all to provocation by over-stimulation, only once or twice each in the course of the work became violently excited and sought, through emotional expression, the sympathetic aid of the investigator.

SUMMARY AND GENERALIZATIONS

1. This experimental study of aspects of behavioral adaptation in chimpanzee was undertaken to discover (*a*) whether, and if so under what conditions, solution of a certain type of novel problem occurs suddenly, as if by discovery and with insight; (*b*) optimal motivational conditions for problem solution; (*c*) whether adaptation to relational problems may be achieved in radically different ways, as by trial and error versus discovery.

2. The Yerkes method of multiple choice, applied by means of a box apparatus, was used for the presentation of six widely differing relational problems to each of four young chimpanzees. The subjects ranged in estimated age from slightly less than four to six years. There were three females and one male.

In terms of relation of the reward-yielding mechanism (box) to the other mechanisms presented for a given "trial," the several problems are definable as (1) left-end box; (2) second from right-end box; (3) right-end box; (4) middle box; (5) alternately the left-end and the right-end boxes; and (6) the same box, no. 5, whatever mechanisms were presented. These problems are described as relational because the only constant and therefore predictable characteristic of the correct mechanism is its spatial relation in a varying group of mechanisms. This definition does not apply to problem 6.

3. Of 24 problem presentations, 14 (58 per cent) resulted in solution. Disappearance of errors was abrupt (following 3 or more errors) in 6 (43 per cent) of the 14 cases. The majority of the remaining 8 successful adaptations were achieved by gradual approximation to perfection of response. Solution, however, may be due to discovery of the essential relationship of the correct box in either abrupt or gradual elimination of errors, but the presumption is in favor of it in the former and against it in the latter. The last statement applies also to ideational process or insight.

4. That problem solution in many instances (approximately 50 per cent) resulted from sudden discovery of the significant relationship and not from the gradual elimination of incorrect responses by blind process of trial is indicated by (*a*) abrupt change in frequency of errors from 30 per cent or more to 0; (*b*) lack of evidence that either the specific settings (groups of mechanisms presented) or the constant order of such settings are learned; and (*c*) ability of the subject to respond correctly with ease and assurance to a new (control) series of settings which differs markedly from the one originally mastered.

5. The chimpanzee subjects exhibited an order of ability to respond to control settings significantly different from that of mammals, other than anthropoid apes and man, for which comparable observations are available. It is noteworthy that the control series of box settings, as contrasted with the regular series, offered certain settings which were new to the subject and also a new order or succession of settings. Under such circumstances of radical change of the situation to be responded to, failure of adaptation, with more or less pronounced emotional disturbance and inhibition of response, might be expected from many types of mammal which are commonly used for psychobiological studies. They did not appear in the chimpanzee subjects of this investigation. Occasionally the apes manifested slight uneasiness or uncertainty, but in most cases they responded to the modified situation with promptness and evident satisfaction and facility.

6. It was the intent of the investigator to discover optimal

conditions for the solution of multiple-choice problems by chimpanzee, not to evaluate specific motivational factors. At various times both rewards and deterrents were used in different forms and combinations. Chief among the former were food, degree of hunger, and social stimuli from companions and investigator. As negative factors (deterrents) appear closing of box doors, confinement in boxes, electric shock, withholding of reward, reduction in amount of reward, presentation of disliked food—each or all as punishment for incorrect responses. These factors were used satisfactorily, but without indication that singly or combined they materially facilitated problem solution. Instead, it appeared that strong positive or negative stimuli were unfavorable to success.

7. The following practically and theoretically significant generalizations are justified by my observations:

(*a*) Motivational factors are of two sorts, barring intermediates and mixtures; (1) those which primarily influence general activity, interest, and alertness, and (2) those which affect specific responses. In this investigation the former appeared to be indispensable, whereas the latter were of slight or even negative value.

(*b*) Given excellent general adaptation to the experimental situation and the experimenter, together with willingness to coöperate by making the circuit through the multiple-choice apparatus a certain number of times daily, marked stimulation by the use of motivational factors interfered with the solution of relational problems by chimpanzee.

(*c*) It is indicated that special rewards and deterrents neither reënforced correct responses nor inhibited incorrect responses, for the fairly obvious reason that the same response might be correct for one setting of the apparatus and incorrect for the next. Seemingly neither reward nor punishment facilitated the selection and confirmation of adaptive response in the multiple-choice situation.

8. Simultaneous use of two subjects in the experiment under conditions which permitted of imitational influence resulted in facilitation of response because of social stimulation. It afforded no evidence that the behavior of the leader, as observed by the

follower, aided the latter in avoiding incorrect choices or in problem solution. The possibility of success by imitation was not realized.

9. The affective condition of the subjects, as suggested by such subjective terms as good will, coöperativeness, optimism, is far more important as basis of problem solution than either degree of behavioral adaptiveness ("intelligence") or specific motivational factors in the form of reward and punishment. Success depends primarily on the maintenance of an organic condition (presumably affective) favorable to that perceptual or ideational process which either constitutes or leads to discovery of the reliable cue to response. For this reason the older or more intelligent individual may fail, while the younger or less intelligent succeeds.

10. The probability of problem solution by discovery varies inversely with the difficulty of the problem. Doubtless this is correlated with the following law of relationship between motivation and difficulty of problem: the more difficult the task, the weaker within limits should be motivational stimuli. Apart from perfect general adaptation to the experimental situation and willingness to coöperate with the experimenter actively and alertly, the chances of solution of multiple-choice problems by chimpanzee are slight.

11. Tests of retention of ability to adapt to multiple-choice problems indicate (*a*) conflict of reactive tendencies due to the presentation of different problems in rapid succession; (*b*) lack of ability to respond correctly to a problem solved some months previously and thereupon followed by work on another problem; (*c*) evidence that a problem whose solution has been lost by reason of conflicts or failure of retention may not be solved more readily on re-presentation than originally. This is a surprise. Probably it is accounted for by the conflicting relations of reactive tendencies acquired in successive problems, and by the influence of the baffling situation upon the affective status or attitude of the subject. Conditions less favorable for conventional measurement of memory and relearning than those offered by this investigation would be difficult to imagine.

12. Predictability of the nature and degree of behavioral adap-

tation, of the achievement of success, or of the order of success by the several subjects of this study, proved to be low. Four groups of data were used singly or in combination as bases of prediction: (*a*) the general behavior of the subject; (*b*) the response and error data for successive series of trials; (*c*) the methods or systematizations of response to specific settings or to a series of settings; and (*d*) the affective and attentional characteristics and status of the subject.

Even when errors decreased to ten per cent, solution remained uncertain. Lack of predictability is believed to be due to the nature of the processes of discovery and of the conditions essential for it. Correlatively, the form of the curve of error (achievement) for chimpanzee in multiple-choice problems varies extremely and is relatively unpredictable.

13. In its endeavor to meet the requirements of this situation the chimpanzee may try varied methods of response in turn; sometimes a method becomes systematized and is used repeatedly despite inadequacy. Usually the several settings evoke different methods of response and establish different reactive tendencies. Certain systematizations clearly result from a native reactive tendency of the subject, whereas others appear to be acquired during work on a problem. Although the methods of response employed may satisfy the requirements of certain settings, they do not ordinarily summate and thus eventuate in problem solution. Trial or testing of methods of response, "trial and error" wise, appears to be essentially different from response on the basis of perceptual (or is it ideational) discovery. The former suggests a groping for the adaptive response; the latter, clear vision of it.

14. Conflict and competition of modes of response may appear in a given problem; they are much more numerous and disturbing when transition is made to a new problem, and they tend to increase as the number and variety of problems presented increase. Occasionally an unadaptive mode of response to a particular setting may persist for weeks, appearing day after day despite severe penalty.

Because of the development of modes of reaction in a given problematic situation which may conflict with those evoked by the next problem, the subject is penalized increasingly by the multiplication of problems. The generalization is suggested by the materials of this report that the probability of prompt solution of a multiple-choice problem diminishes as the number of problems presented (whether or not solved) increases. Beyond the stage of general adaptation to the problematic situation, practice in the multiple-choice experiment does not make perfect.

15. "Learning," as biological process, does not necessarily involve discovery. The latter, as basis of relatively sudden or abrupt solution of a problem, becomes possible only when certain neural structures have evolved in the organic type and have developed in the individual.

16. Discovery, as here used, is believed to be the *anlage* of research activity and essential thereto. Much that is currently spoken of as research is merely information-gathering of the trial and error or behavioral systematization sorts. From such processes those conditioned by discovery differ radically.

Hitherto, in my comparative studies of animal behavior, I have not happened upon forms and characteristics of behavior which obviously presage those expressions of human curiosity and originality which we call invention and discovery.

17. This investigation has demonstrated that habit (acquired reactive tendency versus freedom therefrom) may be the foe of progress; that abundance of part-processes may be unfavorable to the emergence of functional wholes; that the equivalent, physiologically, of open-mindedness in the behavioral realm is conducive to problem solution by discovery.

18. By the results of this investigation I am led to infer that the laws of behavioral adaptation fall within the categories of attention, reënforcement, and inhibition. Various factors and conditions which have been considered important for certain types of habit formation are demonstrably insignificant in the solution of relational problems.

19. The next step logically, if not also practically, in this line of inquiry is to attempt to achieve the factual basis for formulation of laws of adaptation through discovery, and to seek in connection therewith the neural correlates and conditions of such

diverse forms of problem solution as have been exhibited by the application of the method of multiple choice to various primates and other mammals.

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A FIELD STUDY OF THE BEHAVIOR AND SOCIAL RELATIONS OF HOWLING MONKEYS

BY

C. R. CARPENTER
Yale University

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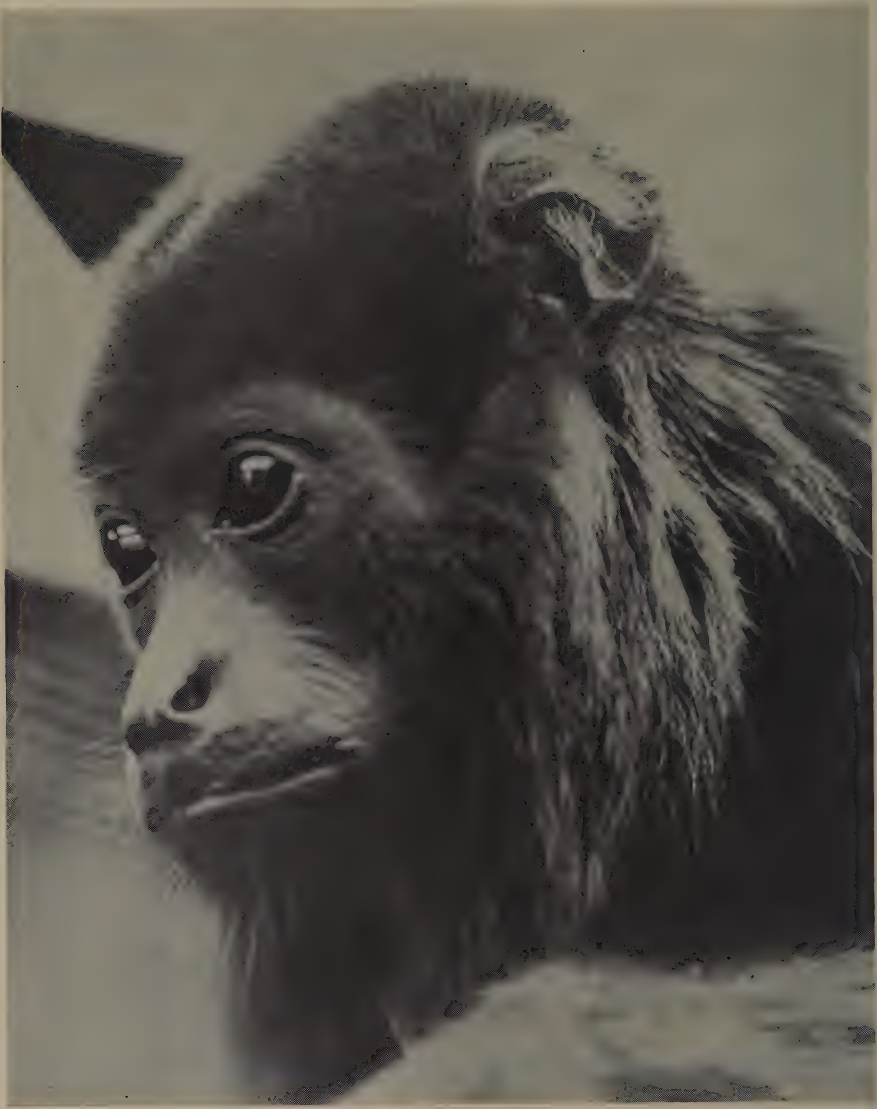

PLATE 1

Portrait of an Adult Female Howler

A FIELD STUDY OF THE BEHAVIOR AND SOCIAL RELATIONS OF HOWLING MONKEYS (ALOUATTA PALLIATA)

C. R. CARPENTER

National Research Council Fellow and Research Assistant, Laboratories of Comparative Psychobiology, Yale University

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I. FOREWORD

Doctor Carpenter's is the third in a series of naturalistic studies in primate habitats, planned in supplementation of the experimental studies in the Yale Laboratories of Comparative Psychobiology. The first of the field studies to be reported was that of Doctor Henry W. Nissen, of the laboratory staff, who, with the generous coöperation of the Pasteur Institute of Paris, initiated work on the social and ecological relations of the chimpanzee in French Guinea.[1] Next in sequence appeared Doctor Harold C. Bingham's account of a field study of the mountain gorilla (*G. beringei*) in relation to its habitat in the mountains of the Belgian Congo. His project was conducted with the coöperation of the

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[1] See reference at end of this report.

Carnegie Institution of Washington. The present report is the first to deal in strictly naturalistic fashion with a New World primate. In plan, procedures, and results, it differs interestingly and instructively from our studies of Old World forms. But this doubtless is in part due to the fact that it pertains to a type of monkey, whereas the earlier reports are concerned with anthropoid apes.

Nearly five years ago my attention was invited by Doctor Frank M. Chapman, universally known and honored ornithologist, to what he considered an extraordinarily favorable opportunity for a field study of howling monkeys in Panama. Subsequently the matter was referred to by Doctor Chapman in our correspondence, and in letter of February 1, 1931, he offers this picture: "In the trees nearly over my house there are at the moment seventeen howlers, three of which are carrying young—a unique opportunity here to study the individual, the family, the clan, and inter-clan relations under a wholly natural but controlled (that is conserved) environment. A year in the field—every day—would yield results." Convinced of the trustworthiness of Doctor Chapman's insight and of the soundness of his judgment, I improved the first opportunity to arrange for systematic observation of varied aspects of the behavior and environmental relations of the howling monkeys on Barro Colorado Island, which has been so effectively and delightfully described as a scientists' paradise in Chapman's volume, "My tropical air castle." During the year 1931, fortunate circumstances rendered it possible to bring into coöperative relation certain of the acts and resources of four wholly independent agencies, the contributions of which may here be described by way of acknowledgment.

First, the National Research Fellowship Board in the Biological Sciences appointed as fellow for work on certain problems of social behavior in primates, Doctor C. Ray Carpenter of Stanford University, who elected during the two years of his incumbency of fellowship to work under my general direction in the Yale Laboratories of Comparative Psychobiology. During a third year he was on appointment as Research Assistant in these Laboratories.

Second, the Barro Colorado Island Biological Laboratory of the

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Institute for Research in Tropical America offered admirable facilities for the projected study of the howler in the habitat which had aroused Doctor Chapman's interest and provoked his recommendation. Although, given the howlers, the island might have been used to advantage without the resources of the laboratory, it would have been much more difficult to do so, and in all probability Doctor Carpenter's results would have been meager by comparison with his actual achievement.

Third, the Committee for Research in Problems of Sex of the National Research Council agreed to coöperate by helping to meet the expenses of an undertaking which, as proposed and as actually carried out, dealt with important aspects of reproductive behavior.

Fourth, our Yale Laboratories supplied the facilities for organization and administration of the project, together with various instrumental and other material aids to the work, and they served in addition as headquarters for the investigator when he was not engaged in field work.

Obviously, this is an unusual constellation of mutually supplementing and reënforcing factors or conditions favorable to discovery. Had the coöperation of any one of the four agencies enumerated failed, the project probably would not have been undertaken.

The report which it is my privilege thus to introduce historically speaks plainly for itself. No one familiar with the pertinent literature on social behavior, and especially with that on the primates, will overlook the unique features of the author's contribution of fact. Because of his opportunity and capacity for sustained, systematic, well-planned, patient observation day after day and week after week, Doctor Carpenter succeeded in gathering data concerning the social behavior and organization, mode of life, and environmental relations of the howlers of Barro Colorado Island which are without parallel, save in our knowledge of man. He made, and in the second year of his field work repeated, the only analytical census of an infra-human primate population of which I have knowledge. The facts are of peculiar interest and value. His is the first reasonably reliable working analysis of the constitution of social groups in the infra-human primates, and of the relations between the sexes and between mature and immature individuals for monkey or ape. He has described in the howler monkey a type of social life and organization which in many features resembles human communism and which in important respects contrasts sharply with the dominance-subordination organization that is manifested in many, if not most, infra-human primates.

In his observational task and in the valuable report which he is presenting herewith, the author unquestionably has made a splendid start on the systematic study of manner of life, nature and conditions of social behavior, of a relatively highly organized form of primate. To attempt to praise him for his devotion to the undertaking and for his notable contribution to our knowledge of a New World monkey would be belittling. Looking forward, it is certain that Doctor Carpenter's contribution may be counted on to command the attention and stir the enthusiasm of other investigators. Probably it will induce some of them to go and to try to do likewise! Another step toward understanding of primate social behavior has been taken. It is a large one. By reason of it we are appreciably nearer adequate basis for determined effort to render new areas of comparative sociology experimental.

We see no reason to be discouraged in the plan of naturalistic research which is an essential part of the research program of the Yale Laboratories of Comparative Psychobiology, and we purpose to press forward in varied directions as opportunities can be made and the necessary resources commanded.

ROBERT M. YERKES.

New Haven, Connecticut,
January 23, 1934.

II. INTRODUCTION

A. ACKNOWLEDGMENTS. I have been assisted in the research of which this monograph is a report by many agencies and individuals. I am indebted most of all to Professor Robert M. Yerkes. He gave me the opportunity to share in an important program of naturalistic studies, adequately supported my project, and en-

couragingly advised me during all stages of the investigation. I am grateful to Dr. Frank M. Chapman for his part in initiating this study of howling monkeys, for his stimulating interest, and for the daily advice which he gave me during the early part of my work on Barro Colorado Island.

During the first two years of this study, I was a fellow of the National Research Council and I owe much to the Fellowship Board for its support. Through the Laboratories of Comparative Psychobiology at Yale University, the Committee for Research in Problems of Sex of the National Research Council aided in financing the investigation. The actual work in the field was greatly facilitated by the services of the Institute for Research in Tropical America, which is directed by Dr. Thomas Barbour and administered locally by Mr. James Zetek. I am thankful to Mr. Zetek for many personal services. I am deeply appreciative of the assistance of Dr. Herbert C. Clark, Director of the Gorgas Memorial Institute. He planned and conducted the first Coto Expedition in which I took part, and he assisted in the arrangements for the second period of observations in the Coto region. I am obligated in many ways to the United Fruit Company and to the Chiriqui Land Company. I am grateful to Mr. H. S. Blair, Manager of the Chiriqui Land Company, to Mr. Jerry Baron, and to Mr. Kenneth Block, for the consideration and hospitality shown Mrs. Carpenter and me while we were their guests. The Secretary of Government and Justice of the Republic of Panama, Colonel Juan Antonio Jimenez, kindly gave me permission to visit the National Reservation of Coiba Island. Señor Feo Cornejo, Director of the Coiba Penal Colony, and Señor J. M. Sifontes were very considerate and helpful while I was making observations on Coiba Island.

I am indebted to Dr. Paul C. Standley for identifying the specimens of foods eaten by howlers. While in the field I benefited by association with Dr. George B. Wislocki and Dr. Robert K. Enders. Professor Robert M. Yerkes, Dr. Henry W. Nissen and Dr. S. Zuckerman have read the manuscript of this report and I am grateful for their valuable criticisms. My wife, Mariana Evans Carpenter, has been of constant assistance to me both in the field and during the writing of this monograph.

B. Purpose of the study. The purpose of this investigation was to secure data on the behavior, social relations, and ecology of the howling monkeys. I planned to study the howler population of Barro Colorado Island in detail. Observations were to be made on the manner in which groups are organized and integrated. In general, problems were to be attacked which could not be investigated feasibly under laboratory conditions. Data were to be sought on food habits, territoriality and nomadism, intra- and inter-group relations with special emphasis on reproductive behavior, and the relation of howlers to their total biotic environment. Attempts were to be made to supplement in every possible way laboratory studies of primates. It was realized from the beginning that the limits of this undertaking would be set by observational and descriptive methods and by the practicability of applying certain procedures of observation to howling monkeys in this particular environment.

The program of studying howling monkeys as originally planned promised to contribute to scientific knowledge in several ways. It was possible that original data might be obtained relative to many current problems in psychobiology, especially problems of behavior and social relations. It was thought that useful information might be gained which would aid in supplementing and interpreting the results of strictly controlled observations and experiments carried out in the laboratory. Improvements might be made in the methods of conducting field studies of primates, and it was hoped that the data secured would suggest new or improved techniques for studying social behavior and social relations in laboratory experiments. Furthermore, it was thought that observations on primates living in their native, and presumably optimum, environment might lead to the definition of significant problems which could be investigated experimentally. The original plans indicated that this study would be supplementary to other research and not independent and conclusive in itself.

C. Location and time of field observations. The first period of this study extended from December 25, 1931, to May 26, 1932, during which time I was in residence on Barro Colorado Island in the Panama Canal Zone. The month of June, 1932, was spent studying the monkeys, including a few groups of howlers, of the Coto region of northwestern Panama. After six months, the study was resumed December 23, 1932, and carried on until February 12, 1933, on Barro Colorado Island. From this date until April 1, I made another expedition into the Coto region and one to Coiba Island off the west coast of Panama to observe the primates, including howlers, found in these regions. The final period of study of the howlers on Barro Colorado Island extended from April 1 to May 12, 1933. About eight months were spent in intensive observation of the howling monkeys, *Alouatta palliata aequatorialis,* in the reservation of Barro Colorado Island, and these observations were supplemented by the study of two other subspecies, *Alouatta palliata palliata* and *Alouatta palliata coibensis.*

D. DESCRIPTION OF BARRO COLORADO ISLAND. Barro Colorado Island is located between 9°8′ and 9°11′ north latitude and between 79°49′ and 79°53′ west longitude. The island lies almost in the center of the Isthmus of Panama in the Canal Zone.

The waters of Gatun Lake, formed by the damming of the historic Chagres River, made islands of many hills, and Barro Colorado Island is the largest of these. It has a shore line of 42.85 miles and a square area of 3840 acres. It is irregular in circumference and approximately three miles in diameter. The island is separated from the mainland at the nearest point by about 300 yards of deep water, including the channel of the Canal. The water level of Gatun Lake is 85 feet above sea level, and the highest point on the island is 452 feet above the level of the lake. The topography of the island is very rugged (see figure 2, pp. 48–49) and many small streams flow from the island to the lake during the rainy season.

Barro Colorado Island is covered by a tropical rain forest. In places the forest is very dense and contains large trees 125 feet or more in height. Other regions are covered with scrub growth and bush. There is a gradual transition in many areas from scrub growth to dense primary forest; however, it is estimated that about two-thirds of the Barro Colorado forest is primary growth.

Barro Colorado Island was made a natural reservation in 1923 by Governor Jay J. Morrow and through the efforts and initiative of Dr. Thomas Barbour and Mr. James Zetek. The Institute for Research in Tropical America was organized for the development and management of this reservation. The Institute has made of the island a very satisfactory location for the study of many biological problems. A launch service connects the island with the railroad to Colon and Panama City, and hence necessary supplies are made available. Comfortable buildings have been erected and are adequately serviced. A network of trails has been cut through the forest and these are kept cleared. Each route is named (see figures 1 and 2, pp. 44, 48–49) and numbers are posted at hundred yard intervals, making orientation on the island and the location of points relatively easy. At the end of six of these trails (see figure 2, pp. 48-49) small houses have been built at the water's edge. They are supplied with water, food, and bedding. The houses afford adequate stopping places for a night, or they may be used as centers from which work in adjacent regions may be carried on for many days.

The fauna and flora of Barro Colorado Island have been described by others: Standley (58), Chapman (17), Kenoyer (42), Goldman (30) and Enders (25). About 1259 species of plants and trees from the island have been identified by Standley. Chapman (17) has observed and listed over 230 species of birds. The studies of Chapman (17) and Enders (26) show that the island has almost a complete sampling of the animals found on the mainland of Panama. Four species of primates are found there, and these species represent four genera. They have been identified as the marmoset, *Oedipomidas geoffroyi*; the night monkey, *Aotus zonalis*; the cebus monkey, *Cebus capucinus*, and the howling monkey, *Alouatta palliata aequatorialis*. The spider monkeys indigenous to Panama are not represented on the island.

There are two distinct seasons in the Canal Zone; the rainy and the dry. The latter covers the months of January to April, although the beginning and end of the dry season vary with different years. During this period, from 7 to 10 inches of rain may fall, and there may be from 100 to 125 inches of rain during the wet season. The dry season is ideal for observational work, and two of these periods were chosen in which to conduct this study of the howling monkeys.

The temperature on the island ranges from 67° to 90°F. The effect of heat on an individual varies greatly during the diurnal cycle because of related humidity and winds. Humidity fluctuates between 75 per cent and 90 per cent saturation. During the dry season, the trade winds blow almost constantly and, in general, the climate is fairly comfortable.

E. CLASSIFICATION AND DESCRIPTION OF HOWLING MONKEYS STUDIED. Elliot (24) lists the howling monkeys in the family *Cebidae*, sub-family 1, *Alouattinae*, and genus *Alouatta*. The *Alouattinae* are thus characterized by Elliot (24, p. 258): "Head pyramidal; body thick, heavy; face naked; chin bearded; tail long, prehensile, naked at tip; thumb opposable. Skull: braincase depressed; occipital region truncate; angle of mandible enormously developed; lower incisors vertical; canines rather strong; claws convex, powerful; hyoid greatly inflated."

The species *A. palliata* Slack, according to Elliot (p. 272), is characterized as follows: "Face naked; hairs on forehead short, stiff, upright; those on back of head longer; beard moderate." He describes the color thus: "Head, throat, shoulders, arms, legs, hands, feet and tail black, with a tinge of maroon; middle of back and upper part of sides black mixed with golden; lower parts of flanks, hairs much lengthened, yellowish brown, base of hairs much paler; under parts very sparsely covered with dark chestnut hairs. . . . . Some specimens are entirely black." This classification would include the mainland forms observed in this study and those on Barro Colorado Island.

Elliot classifies the howling monkeys of Coiba Island as *A. p. coibensis* Thomas. He describes *A. p. palliata* as being similar in general characters to Coiba howlers except that the latter are smaller. The color is described (p. 273) as follows: "Head, upper part of back, arms, legs, hands, feet, and tail black; middle of back Prout's brown, hairs tipped with golden; long hairs on flanks shining ochraceous buff; abdomen dark brown."

While the field work of this study was in progress, Miss Barbara Lawrence at the Harvard Museum of Comparative Zoology was revising the classification of the *palliata* group of howling monkeys which includes the three subspecies of howlers on which observations were made. Lawrence summarizes her paper (p. 342) as follows: "Seven sub-species of *Alouatta palliata* have been recognized here, *A. p. palliata,* from Costa Rica, Nicaragua, and Honduras, *A. p. aequatorialis* from Panama and the Pacific coast of South America as far south as Ecuador, *A. p. trabeata* subsp. nov. from the Azuero Peninsula in Panama, *A. p. coibensis* from Coiba Island of the Pacific coast of Panama, *A. p. pigra* subsp. nov. from northern Guatemala, *A. p. luctuosa* subsp. nov. from British Honduras, *A. p. mexicana* from the Vera Cruz Province in Mexico. Subspecific variation amongst these monkeys is notably very small and individual variation is relatively great. For this reason groups are separated on the basis of average differences and in most cases extreme individuals may be found in each group that resemble very closely individuals of some other subspecies. This is especially true of *A. p. palliata* and *A. p. aequatorialis,* and in Panama transitional forms are found that are very intermediate between the two. *A. villosus* Gray has been discarded owing to the imperfect condition of the type, and the impossibility of determining the type locality. *A. p. inconsonans* (Goldman) proves to be synonymous with *A. p. aequatorialis.*"

This monograph deals chiefly with *A. p. aequatorialis* Festa, but also some observations were made on *A. p. palliata* Gray and *A. p. coibensis* Thomas. Specimens collected by me in the Canal Zone, the Coto region of northern Panama, and Coiba Island were used by Lawrence, and hence this identification is in accord with her classification. Observations on animals other than *A. p. aequatorialis* were made to learn whether there were differences in behavior and social grouping among subspecies. It was thought desirable, also, to make some comparisons with other species.

Lawrence (44, p. 323) describes *A. p. aequatorialis* as follows: "General color back to dark mummy-brown, with the mantle hairs . . . . golden 'ochraceous'; the back is evenly sprinkled with a varying number of light-tipped hairs, and there is a slight scattering of light-tipped hairs on the tail especially on the under surface; . . . . ". Lawrence emphasizes the great range of color variations between the extremes of almost pure black to dark mummy brown and walnut.

There are marked color variations in the howlers of Barro Colorado Island and on the mainland. It was my impression that there was somewhat less variation in color among the Coiba howlers. There are marked variations in the subspecies according to age and sex. The new-born animal is a grayish brown (see plate 15, A to I). This color gradually changes to dark sprinkled with light and brownish hairs. When the young animal is between ten and twelve months of age, the reddish-brown mantle hairs begin to appear, as shown by a captive animal of known age. The mantle is longer and more colored in adult males than in adult females. There are a few individuals which are uniformly dark in color, and there are others which have marked reddish-brown coloring extending over the sides and back. Both on Barro Colorado Island and Coiba Island there are individuals with yellowish-white bands on their tails; however, these variations are rare. Two animals with banded tails were observed in the same group on Coiba Island. In some instances, other types of coloration are more uniform in a single group than in a large population including many groups. This fact would seem to indicate a higher degree of inter-breeding within a clan than occurs among groups.

Male howlers are somewhat larger and heavier than females of the same age. Schultz informs me that this difference is shown most clearly in measurements of chest circumference. The adult males of *A. p. aequatorialis* range in weight from about 16 to 20 pounds, and the adult females range in weight from approximately 15 to 18 pounds. From fifteen measurements of total length of males (*A. p. aequatorialis*) given by Lawrence (44), the average was found to be 1146 ± 57 mm. Sixteen adult females were measured and the average total length found was 1111 ± 39 mm. The difference in total length is suggestive, but not highly significant. Probably because of the longer hair, and especially the longer mantles and beards, adult males appear larger than they actually are, and they may be readily distinguished from adult females.

Lawrence finds much overlapping and similarity between *A. p. palliata* and *A. p. aequatorialis.* The examples of *A. p. coibensis* and *A. p. trabeata* are more distinct, according to her, although the significance of measurement differences was not calculated. Obviously, the accurate differentiation of subspecific differences is a difficult taxonomic problem.

III. REVIEW OF LITERATURE ON THE NATURAL HISTORY OF HOWLING MONKEYS

A. SELECTED OBSERVATIONS ON HOWLERS. Some of the early explorers, colonists, and soldiers who went into Central and South America in the sixteenth and seventeenth centuries report their experiences with howling monkeys. To typify these descriptions, I have selected a quotation from the writings of Captain William Dampier (19). In volume II of his "Voyages and descriptions," Part 2, p. 59 addressed to the Right Honorable Edward Earl of Oxford in 1700 (from notes of 1676), he gives the following description of "large Monkeys": "The Monkeys that are in these Parts are the ugliest I ever saw. They are much bigger than a Hare, and have great Tails about two Foot and a half long. The under-side of their Tails is all bare, with a black hard Skin; but the upper-side, and all the Body is covered with coarse, long, black, straight Hair. These Creatures keep together 20 or 30 in a Company, and ramble over the Woods; leaping from Tree to Tree. If they meet with a single Person they will threaten to devour him. When I have been along I have been afraid to shoot them, especially the first Time I met them. They were a large Company dancing from Tree to Tree, over my Head; chattering and making a terrible Noise; and a great many grim Faces, and shewing antick Gestures. Some broke down dry Sticks and threw at me; others scattered their Urine and Dung about my Ears; at last one bigger than the rest, came to a small Limb just over my Head; and leaping directly at me, made me start back; but the Monkie caught hold of the Bough with the tip of his Tail; and there continued swinging to and fro, and making Mouths at me. At last I past on, they still keeping me Company, with the like menacing Postures, till I came to our Huts. The Tails of these Monkeys are as good to them as one of their Hands; and they will hold as fast by them. If two or more of us were together they would hasten from us. The Females with their young ones are much troubled to leap after the Males; for they have commonly two: one she carries under one of her Arms; the other sits on her Back, and clasps her two Fore-Paws about her Neck. These Monkeys are the most sullen I ever met with; for all the Art we could use would never tame them. It is a hard matter to shoot one of them, so as to take it; for if it gets hold with its Claws or Tail, it will not fall as long as one breath of Life remains. After I have shot at one, and broke a Leg or an Arm, I have pitied the poor Creature to see it look and handle the wounded Limb, and turn it about from side to side. These Monkeys are very rarely, or (as some say) never on the Ground." This description is of the howlers which range about 18° north latitude in Nicaragua and apparently refers to the species *A. p. palliata*. The quotation from Dampier is an excellent and interesting historical example of naturalistic descriptive writing on animal behavior.

A century after Dampier's vivid experience with howlers, Don Felix de Azara (5) was, in his leisure time from 1782–1801, observing the howling monkey or *Caraya* as well as other animals of Paraguay. The Caraya of Paraguay, termed by Linnaeus *Simia Bulzebut*, by Buffon *Ovarine*, and by La Cepédè *Alouatte heuleur*, derives its name from the word *Caaya* which means "chief of the woods," according to Azara. He states that they are abundant in the thick woods of Paraguay and are the largest of the monkeys found there. Azara describes them as melancholy, slothful, heavy-looking animals which live in families of from four to ten. "Each male," writes Azara, p. 2, "takes charge of three or four females, and if the band consists of from eight to ten (which is the largest known), there are three males." Azara points out that color similarity of young males and adult females may account for the above finding in part, for there may appear to be more females at first sight than there actually are, since young males may be mistaken for adult females. The families are "directed" by the males as the animals move from limb to limb without jumping. They may drop their excreta on a person underneath them, and this is accounted for by Azara as a result of fright, but he says, "some attribute their so doing to malice." They hide themselves when afraid, observes this author, and seem to prefer the tallest trees. "Some persons," wrote Azara, p. 3, "assert that they have seen them take leaves, chew them, and apply them to their wounds; but in those which I have killed and wounded, I have never observed anything of the kind. . . . Their powerful, melancholy, harsh, insufferable, and indescribable voice is heard" in the early morning and evening, and Azara estimates that it may be heard at a mile's distance. He was unable to learn whether the vocalization is produced by "all the family or only . . . the chief," although he believes the entire family participates in the production of the howls. He says that they ceased howling when approached. Caraya are rarely domesticated and Azara believes this is either because of their disagreeable voices or ugliness and slothfulness. Caraya, according to Azara, give birth to one young in July and the infant is carried by clasping its arms around the neck of the mother. Azara relates having observed a guide yell at a band saying, "Ha hijo de puta," a highly insulting remark. One of the females threw her baby to the ground. He says that the same thing would have happened had other words been used. Caraya are reported to eat leaves, fruit, insects, and wild bee honey. The opinion was current that the animals might descend to the ground to rob corn fields, but Azara did not observe this action. He gives a creditable account of the general appearance of an adult male and points out that the females are smaller, have a shorter beard, less enlarged larynx, and a whitish vulva. The English translation of Azara's observations made by W. P. Hunter in 1837 concludes with the unique account of Azara's having seen an albino individual, "that is, one altogether of a yellowish white color." The French translation of Azara's writings by M. L. E. Moreau-Saint Méry in 1801 contains a discussion of former classifications of Caraya and comments on the work of Buffon.

An abridged edition of M. de Buffon's (15) classical natural history published in 1791 contains an account of the "warine and the alouatto . . ." The reports of Marcgrave are of historical interest and they run as follows: One of a group signals with his hand and the others gather around, and as soon as they are seated he begins an "oration." When he has finished, he signals the rest to answer him and they cry together until he again causes them to be silent by a motion of his hand. Thus Marcgrave describes the howls of the mornings and evenings which are commonly heard. Females are reported to carry their young on their backs, and the young one holds on by clasping its arms around "the lower part of the body of the mother." Marcgrave believes that the animals were wild and could not be tamed or subdued. They are supposed to feed on fruit, grain, and insects. The story continues to the effect that if one is wounded, the rest of the group assembles around it and "clap their fingers into the wound. If then the blood flows in any quantity they keep it shut up, while others get leaves which they chew and thrust into the orifice." Marcgrave reports that females give birth to only one young. Many observations similar to those of Marcgrave appear in naturalistic literature.

Humboldt and Bonpland (38) report significant and original observations on a species of howler in their publication of 1811, "Recueil d'observations de Zoologie et d'Anatomie Comparèe." According to Humboldt, *Simia seniculus* is the most abundant of all group-living primates of the torrid zone. More than forty were observed in a single tree in the region visited, and Humboldt estimates that in a square league, two thousand of these primates may be found! The eyes, voice, and gait denote for Humboldt melancholy. The young ones are not reported to play like other monkeys. Forbes (28, p. 194) quotes the following interesting passage from Humboldt's descriptions: "We stopped to observe Howling Monkeys, which, to the number of thirty or forty, crossed the road by passing in a long file from one tree to another upon the horizontal and intersecting branches. . . ." Again he writes, "On approaching a group of trees, we perceived numerous bands of Arguatoes going as in a procession from one tree to another with extreme slowness. A male was followed by a great number of females, several of which carried their young on their shoulders. . . . It is most superfluous to add how dubious is the assertion that Arguatoes and other monkeys with prehensile tails form a sort of chain in order to reach the opposite side of a river. We had opportunities, during five years, of observing thousands of these animals, and for this reason we place no confidence in these stories."

Rengger (53) in his "Naturgeschichte der Saugethiere von Paraguay," characterizes the behavior of *Mycetes Caraya*, the howling monkey which Elliot has termed *Alouatta caraya* Humboldt. This book, published in 1830, one hundred years before the present study was begun, contains very complete descriptions of howling monkeys.

Rengger found Caraya in dense forest, even in high altitudes near stream beds, but they were seldom located in dry regions. An entire day might be spent by them in a single tree. Their food, Rengger observes, consisted principally of leaves and buds, but also of fruits and insects. In emergencies, the animals might eat bark. They are reported to be strictly arboreal, for Rengger saw neither the animals nor their footprints on the ground.

These howlers were observed by Rengger to live in families which, exclusive of the young, always contained more females than males . . . "im Allgemeinen kann man drei der ersteren auf eines der letzteren rechnen." This proportion is not natural, he says, because among the young equally as many males as females are found. He accounts for this fact on the basis that males are more conspicuous and approach hunters more closely than females; hence males are killed more often by natives than are the females, and this causes a disproportionately large number of females remaining in the groups.

The animals, according to Rengger, are slow and sluggish in locomotion and climbing; the four hands and tail are constantly in use. They lack the agility of either Cebus or Ateleus, and do not swim. Rengger saw in one instance a group in a single tree isolated by water sixty feet wide, and although they had eaten all the leaves and part of the bark from the tree, yet they would not cross the sixty feet of water to the fresh forest where there was an abundance of food.

Rengger, following Humboldt (38), describes the sex difference in structure and function of the vocal mechanism. The roars, he says, are produced by more than one animal and are initiated by a male. Following this, the females join in with weaker voices. Rengger agrees that Azara (5) had aptly described the roars of howler males as being like the squeaking of the wheels and axles of an American wagon. The roars occur morning and evening, and especially during warm weather; however no causes for these vocal outbursts were found, and Rengger supposes that, as in birds, the howling is a kind of music which the animals produce and enjoy. This opinion is quoted with approval by Charles Darwin (20).

According to Rengger, the females give birth to single infants between the last of May and the first of August. For several weeks the infants are carried near the breasts and then they are found riding on the mother's back. The mother and young are always close together. Never, writes Rengger, do howlers play with one another; thus he is in agreement with Azara on this point.

Rengger states that the ugliness and difficulty of taming result in howlers seldom being taken captive for pets, and that usually captive howlers die within a few months. During the six years of his stay, this naturalist saw only two howlers in captivity. They were of different ages, were fed leaves, and were active only when seeking food. These animals were no more friendly to their keepers than to strangers.

The same author states that the enemies of Caraya, besides man who kills them for food, are the puma and the ocelot, and he estimates that howlers may live fifteen or twenty years.

Wallace (63) traveled on the Amazon and Rio Negro of Brazil in the middle of the nineteenth century, and came into contact with many howling monkeys. He noted that species of monkeys may have limited geographical ranges, the borders of which are often mountains or rivers. In his "Tropical nature and other essays" (65) Wallace writes, p. 118: "The most remarkable of the American monkeys are the howlers, whose tremendous roaring exceeds that of a lion or bull, and is to be heard frequently at morning and evening in the primeval forests. The sound is produced by means of a large, thick, boney vessel in the throat, into which the air is forced; and it is remarkable that this one group of monkeys should possess an organ not found in any other monkey or even in any other mammal, apparently for no other purpose than to be able to make a louder noise than the rest." Wallace denies the truth of Humboldt's observations that more than one animal joins in producing the roar. It is his opinion, judging from the suddenness with which the sounds begin and end, that only one animal, generally a full-grown male, produces the howls, but as we shall see later, Wallace is wrong in this, just as he is incorrect regarding the function of the howls.

Additional observations on the howler, *Alouatta villosa* or *Mycetes villosa*, are reported by Godman and Salvin (29). These howlers are to be found in companies of five to six individuals. They range in the higher arboreal altitudes and move sluggishly away when approached by an observer. Regarding the distance the voice travels, Salvin writes, "It would certainly not be over-estimating the distance to say two miles." He estimates that when the sound passes over a lake or is unhindered by forest, it can be heard about a league away.

Bates (8) made an observation and inference of significance. "It does not appear," he writes, "that their [howlers'] harrowing roar is emitted from sudden alarm; at least it was not so in captive individuals. It is probable, however, that the noise serves to intimidate their enemies." Belt (9) in his book, "The naturalist in Nicaragua," reports that the howling monkeys (*Mycetes palliatus*) called by the natives "congo", were rarely seen because "they generally remain quiet among the upper branches of particular trees" and presumably are not detected.

Brehm's *Thierleben* (11) of 1876 quotes Hensel to the effect that howlers are found in small troops of from five to ten individuals, and that these troops have a small territorial range which they rarely abandon. In each troop at least one adult male is found. It is Hensel's opinion, contrary to that of Azara and Rengger, that young are born during the entire annual cycle.

Goldman (30) writes, p. 229, of *A. p. aequatorialis* (listed by him as *A. p. inconsonans*) that they occur in small numbers near Gatun of the Canal Zone. "On Cerro Azul a troop of about twelve was found in a group of very tall trees. The troop included several full-grown males, females and young. A very young individual was seen clinging to the lower part of its mother's back as she climbed into topmost branches along with other females and young animals." One group was seen on several occasions in the same region. Howling occurs after daylight and at intervals during the day, according to Goldman, and vocalizations also occur at the beginning of showers of rain. Goldman describes the howls as "a series of deep growls, becoming a prolonged roar when given by several in unison . . . ."

Chapman (17), who has made observations on howlers for many years incidental to his study of birds, records many facts pertinent to this study. He raises the question of why monkeys react as they do to man. He records the compactness of howler groups and suggests that in their social relations, howlers are phlegmatic and peaceful. They are restricted to first growth forest, according to Chapman, and he infers that groups have limited territorial ranges. He describes the howling as follows: "Beginning as a low grunt, it grows louder, rapid, more incisive, and quickly rises to an overpowering, ferocious-sounding roar." This observer indicates several stimulating situations which result in howlers roaring. Relative to group composition Chapman writes that there are usually one or two adult males, a young male or two, and the remainder of the clan consists of females and young. Chapman estimates that the average clan contains about ten individuals, and on the basis of this estimation, he suggested that there were probably seventy howlers on Barro Colorado Island in 1929. Observations are given of males and females retrieving a baby. The descriptions of howlers presented by Chapman are equally as valuable and stimulating as those of Azara and Rengger.

The naturalistic literature on howling monkeys contains many repetitions of observations and inferences. I have considered it unnecessary to review every report but I have selected the most important ones and those which are relatively reliable and of historical interest. As the following summary will indicate, many very important facts are known of the natural history of the howling monkeys.

B. SUMMARY OF THE LITERATURE ON HOWLING MONKEYS.

Habitat. Howlers range from about 30° south latitude to approximately 35° north latitude, and from sea level up to six thousand feet altitude. They are restricted to Central America, northern South America, and a few islands on the coasts, e.g., Coiba and Trinidad. The animals prefer dense primary forest and apparently do not cross water or open country. One author reports that howler groups are adapted to specific territory.

Physical appearance. Howlers are described as being very large and "ugly." They are said to approach in size some of the Old World baboons. They have long prehensile tails, and the males particularly have conspicuous beards. The mantle has sometimes led to their being called "mantled howlers."

Temperament. Howlers are rarely kept in captivity, presumably because of wildness, and also because they soon die. They are said to be serious, slothful, melancholy, phlegmatic, and peaceful. They are, even when juveniles, extremely difficult to tame.

Vocalizations. The "howl" is a most conspicuous form of howler activity. The main vocalization is described in various ways as a howl, a roar, a barking roar, drum-like, and like the squeaking of an American wagon. Also, this vocalization has been described as powerful, melancholy, insufferable, and indescribable. It has been supposed to serve no useful function whatever, to correspond to the song of birds and be a kind of music, to be an expression of emotions, and to serve the function of defense.

Locomotion. The locomotion of howlers is reported to be slow and sluggish, and during this activity all five appendages are constantly used. They are said to jump minimal distances and to travel in single file. Previous opinion has been that howlers rarely come to the ground and will not swim.

Groupings. Howlers are generally known to be gregarious and to live in groups varying in size from four to ten individuals according to some; from five to ten according to others; and even from twenty to thirty. Several authors report that there are a few males in each group, and some observers hold the opinion that howler females outnumber males by about a three to one ratio.

Intra-group relations. Howler groups are supposed to be led by males. Babies are carried first on the ventral, then on the dorsal, surfaces of the mothers. The number of young born seems to be one, but there is much uncertainty regarding the periodicity of reproduction. Howlers are not supposed to be monogamous. Both males and females have been observed retrieving young which had fallen.

Reaction to an observer. It is generally believed and reported that howlers react vigorously, and some suppose aggressively, toward an observer. Howlers apparently may drop waste matter on an observer. One author believes that the reaction to an observer is motivated by anger and bluff rather than fright.

Enemies. Man is thought to be the howlers' most serious enemy. Pumas and ocelots are also postulated as probable enemies. Little is known of how seriously diseases or parasites affect the mortality rate of howling monkeys.

IV. FIELD PROCEDURES AND REACTIONS OF HOWLERS TO AN OBSERVER

The particular procedures employed in a field study are determined largely by the type of animal to be observed and the kind of environment in which it lives. Different genera of the same family may not be observed in the same way. For example, groups of spider and howling monkeys may be followed and observed for hours or even days, but to do this with capuchin monkeys would be impossible. Since one is forced to use different procedures with different genera, comparable data are difficult to secure.

Field work on the behavior of primates in the wild requires special training, just as special training is necessary for the collector, the student of bird life, or the field anthropologist. One soon learns that collecting cannot be carried on entirely successfully along with a program for the observation of primates. To a lesser degree, photography is incompatible with many observational procedures. The field worker also learns that there are ways of observing his particular subject which yield him the most information of a reliable kind.

A. Equipment and procedures used in this study. During the study of the howlers, the following instruments and materials were always accessible and, with few exceptions, were carried daily: field glasses (Marlux 8-power), pocket notebook and pencil, camera (Leica model D with 135 mm. telephoto lens), pistol (Colt automatic .32 caliber), compass (small pocket), machete, snake kit with antitoxins, clean cloths, canteen, and water-proof bag. A shot gun, steel tape, and dissecting instruments were carried when specimens were to be collected. For special photography an Eyemo motion picture camera and two types of Graflex cameras were used. Equipment was selected which was light and compact, and which the observer himself could carry.

The procedures which I have used in this study have been guided by well defined objectives. General objectives and specific questions were formulated and kept in mind and observations were made relative to about one hundred of these questions. Realizing that the normal behavior of wild animals might be completely distorted by the presence of an observer, attempts were made to observe the animals with a minimum of disturbance. It was desired to observe the activity of howlers as it would have occurred had there been no observer present. Also, since I was mainly interested in social behavior, attempts were made to observe simultaneously the largest possible number of animals for the longest possible time. Brief notes were made immediately following significant observations, and these notes were rewritten in detail while the incidents were distinctly recalled. Furthermore, an observation was finally accepted only after confirmation and re-checking, and if all details necessary for a reasonable interpretation were known. Observations which resulted from following these guiding statements and criteria were written up systematically according to subject and were used in the preparation of this monograph.

The procedures used in the study of the howling monkeys may be stated and briefly described as follows:

Procedure 1. Direct observation with complete concealment of the observer. Temporary blinds, made of green burlap and brush, were constructed both in trees and on the ground at places frequently visited by howler clans. When animals approached it was possible for me to hide myself in the blinds and to observe the animals by the use of field glasses without disturbing them. Howlers eventually showed no noticeable reactions to these blinds, perhaps, in part, because of the camouflage structure and coloring and their constant presence in the forest.

Procedure 2. Direct observation from ambush. I took advantage of banks, rocks, bushes, and tree trunks to conceal myself. In certain situations it was possible by this method to observe animals for hours without distracting or disturbing them. Field glasses permitted me to remain at a distance and yet to have the advantage of a closer view.

Procedure 3. Direct observation following neutral conditioning of the animals to the observer. If an observer remains near howlers for a long period of time, daily for a month or more, they become somewhat neutrally conditioned or adapted to him, and react minimally when he is present. They may be said to behave almost normally while being observed even though an observer is very near them. This procedure was followed in the intensive observations on Group 1 of Barro Colorado Island, and I consider it a method of great value in getting a true conception of characteristic behavior of wild animals.

Procedure 4. Indirect observation: the study of spoor. The remains of dead animals, places where blood had been spilled, excreta, waste from feeding and, in general, behavior resultants whose causes were not directly observable, were all studied carefully for any cues which might be given as to particular kinds of behavior or its interpretation.

Procedure 5. Experimentation. This method was used very little but may be developed. For example, particular animals, such as one or more male leaders, may be removed from a clan and the resulting changes in the group studied. Marked animals which are strangers to a particular group may be released near that group and the consequences studied. In some locations it would be possible to capture, mark, and release a number of animals, after which their life histories in general might be followed. No animal with which I have dealt could be controlled to the extent of causing it to react to apparatus constructed and placed in its range, but this may be possible with some other species of primates.

Procedure 6. Photography: a. Still. Photographs were made from blinds as well as while animals were being closely followed. A lure in the form of an infant howler was once used to cause animals to approach the ground and to move to a place suitable for photographing them. b. Motion picture. Moving pictures of the most prominent modalities of behavior were sought, essentially by the same procedures employed in still photography. Blinds and high powered telephoto lenses were used to advantage. The films when printed served mainly illustrative purposes, but they also aided in checking and validating observations.

Procedure 7. Collections: a. Animal specimens. Animals were collected from clans not under observation on the mainland, and were used for purposes of identification and for detailed study of the appearance of individuals of different age and sex. Four animals were killed on Barro Colorado Island, by special permission, in order to study bot-fly infection and to secure reproductive tracts of oestrous females for histological work. In addition, a series of young animals should have been collected for purposes of identification and classification, but this was not possible. b. Live animals. During this study, a young adult female and two infant howlers were obtained and have been observed in captivity. The female was studied for about two months and then she escaped after swimming to freedom. One infant was kept for three months and then it died; the other infant is still under observation and is now (May, 1934) fourteen months old. Study of these animals at close range has been very helpful in classifying the animals observed in the wild, and it has aided me in understanding and characterizing howler activities. If possible, it is desirable that one be acquainted at close range with primates to be studied in the wild. c. Plant specimens. A collection was made of specimens of food eaten by howlers. These plant specimens were preserved, numbered, and sent to a specialist on Central American flora for identification.

B. Reactions of howlers to an observer. Different groups of howlers on Barro Colorado Island, on the mainland of Panama, and on Coiba Island react differently to observers. There are types of reactions ranging from fleeing and concealment to bluff and aggressive behavior. Usually, however, howlers do not flee very far, and it is possible for an observer to remain with a group as long as he desires. The males almost always come to the border of the clan nearest to the observer and roar with reference to him. However the following observations will typify the reactions of howlers to man:

Observation 1, Jan. 8, 1932, Group 1. Interference from the observer decreased the average rate of progression, reversed the initial direction of movement, and caused a shift in the males which led the clan. The result was that the group fed from different trees and spent the night in a different area from that toward which it first moved. The entire character of the group's activity was changed apparently by disturbance from the observer.

Observation 2, Jan. 15, 1932, Group 1. A male suddenly came into full view as I was attempting to conceal myself. He vocalized in a deep gurgling sound that was repeated immediately afterwards by other males which could not have seen me. All animals of the group ceased activity and assumed defensive attitudes or positions of concealment while reacting constantly with reference to the observer and the dominating clan males. Several hours later, evidently when they were more strongly motivated by hunger, they moved into other near-by trees and fed.

The animals of Group 1, after I had made many contacts with them, became neutrally conditioned or adapted to me in 1932, and my presence affected them minimally. When I approached them, feeding, play, or progression continued and no defensive roars were given. Since I did not harm the animals or behave aggressively toward them, defensive responses disappeared to a large extent. When I returned to the island six months later, roars did not occur when I met the clan, but I judged the animals to be wilder than when I left them the previous May.

The different groups of the island behave differently toward the presence of human beings. In general, those groups located where they have had frequent contacts with man react least vigorously to him. Groups which range in parts of the island where people rarely, if ever, go, for example one thousand yards west of Fuertes House, react to a person either by vigorous howls or by avoidance and caution. The following notes may illustrate the point:

Observation 3, April 17, 1933, Group 10. After initial howls provoked by my approach, the males became extremely hesitant about beginning progression. Five hours of continuous observation, much of the time under cover, were necessary before I could make a count of the group. The males would sometimes approach to within 50 feet of me and evidence "investigatory" and "rage" behavior; that is, they would repeatedly look at me from different positions, roar, shake branches, and defecate.

Observation 4, Jan. 15, 1933, Group 11. As I approached this group, vigorous and repeated roars were given by the clan males. The other animals of the group stopped moving and crouched on limbs watching me. From 10:00 until 12:00 o'clock the intermittent roaring barks were given, and during this time the clan had moved only about 25 yards.

From my study of the howlers of Barro Colorado Island, on the mainland of the Canal Zone, near Puerto Armuelles, in the Coto region, and on Coiba Island, I can differentiate four types of general reactions to man: (1) The animals which have had frequent and long-continued contact with a person or persons who did not disturb them, react neutrally to an observer; that is, by neither withdrawing nor reacting aggressively. This behavior is characteristic of several groups on Barro Colorado Island. (2) The animals which have had relatively frequent contacts with man react to him by howling and exhibiting mild "rage" behavior which soon ceases and, otherwise motivated, the groups continue feeding, progression or resting and sleeping. (3) The animals which have had very infrequent contacts with man vocalize when approached; the males become aggressive and the females and young react specifically to the observer. The entire activity of the group is distorted by the presence of a man, for the animals react as they would to an attacking enemy. (4) The animals which have been hunted and shot at respond to the approach of a man by becoming quiet; no vocalizations are given, and the animals conceal themselves or flee for short distances into the tops of trees. This kind of reaction is typical of howler groups on the mainland in the Canal Zone, near Puerto Armuelles, and on Coiba Island, where they have been hunted.

When an observer is very close to some groups of howlers, two significant types of behavior may be seen. An animal may break off dead limbs and drop them, or fecal matter may be released with reference to the observer. On occasions, I have seen adult howlers, usually males, while showing vigorous reactions to an observer, break off a dead limb and then drop it toward him. At times, the animals behave as if selecting a limb which may be broken and dropped. The forepaws are used to pull and wrench the piece of wood free, and then it is dropped toward the observer while the animal is watching him. The object is rarely moved away from where it was attached but is merely broken and released at a point nearest the observer.

That monkeys defecate and urinate when frightened is a common observation. Captive howlers defecate when greatly excited. In the wild, there is a certain directedness about this behavior which seems to indicate processes of central nervous system control. I have observed a dozen or more cases of howlers, usually adults but in one instance a juvenile, which behaved as follows: I would usually be sitting quietly observing the animals as they were in the trees above me. Either seen or unseen, an individual would slowly approach to a place directly above me or as near-by as possible, and then would release excrement, either urine or fecal matter or both. When the act was completed, the individual would usually quickly withdraw. While observing animals from within a blind located under the line of march of a group, I have seen as many as half of the animals release fecal matter on the blind as they crossed over it. The animals would stop, complete the act, and then hurriedly continue. The behavior of stopping and remaining for as long as a minute over a near-by disturbing object is behavior inconsistent with a flight reaction. Seemingly, the dropping of branches and excrement are kinds of primitive instrumental acts.

When howlers are approached by an observer they frequently yawn with a slow inspiration of breath. This behavior occurs when animals are greatly excited.

C. SUMMARY. The guiding principles of the procedures used in this study have been considered as well as details of different types of observational procedures. Examples of observations on the way howler clans react neutrally to an observer, that is, without distinct positive or negative behavior, have been offered. Howling roars and bluff may be shown for a short or long period of time or howler clans may flee for short distances and climb to the topmost branches of trees. Two types of defensive behavior occur, namely, the breaking and dropping of dead branches and the release of fecal matter and urine with reference to the observer.

V. MANIPULATION, POSTURING, LOCOMOTION, AND FEEDING

Observations of the ways in which animals manipulate objects, adjust themselves to supports, move and feed, correspond to the study of motor skills in human subjects. These kinds of detailed action characterize the behavior of specific types of animals, and studies of the finer motor patterns may supply some information regarding the animals' relative capacities and adaptability. Special behavior capacities of different primate types may also be defined by close study of their motor skills.

A. MANUAL DEXTERITY. That primates differ widely in the ways they use their hands, feet, and tail is generally known. In the platyrrhines alone great diversity is found. Spider monkeys have only four fingers (about 5 per cent have a rudimentary thumb, according to A. H. Schultz) which are used as a very adaptable hook, especially effective in the brachiating form of locomotion. The capuchin monkeys use their hands in a human-like way, the thumb being opposable and objects are held in the hand with apparent ease; whereas the hand of the howler monkey functions differently from that of any other primate which I have observed.

Observations on the use of the howler's hand show: (1) that the thumb is not opposable, (2) that there is a concentric movement of the fingers toward the object with the thumb and first digit opposing at a sharp angle the second, third, and fourth digits, and (3) that there is a functional division of the hand between the first and second digits. All fingers flex slightly toward the midline of the palmar surfaces.

The way in which the howler's hand functions is a characteristic of the new-born animal as well as of the adult (see plates 14, A, and 15, B). The finer movements of prehension necessary for grasping a small object are poorly coördinated. The *concentrically functioning hand* characteristic of howler manipulation is adequately suited for their pronograde form of locomotion. Study of the functions of the fingers show that when a howler moves down a limb, the hand is placed in such a manner that the thumb and first digit or index finger are on one side, and the second, third, and fourth digits are on the other side of the limb. The weight is then equally balanced along a line approximately in the center of the palm. The fingers in this way effectively grasp the oval surface of the limb. The concentric type of manipulation also relates to the manner in which the animals feed.

Observations on handedness were made, but the results are inconclusive. It is my impression that howlers in the wild are ambidextrous, but the opinion needs substantiation.

B. USE OF FEET. The feet of howlers are well fitted for grasping the branches of trees, trunks, limbs, and vines in the forest habitat. The great toe is opposable to the other digits (see plate 16, B). Howlers grasp limbs and vines, with ease and sureness, between the great toe and the other digits. The structure of the feet is poorly adapted to flat surfaces, as is shown by observations of captive animals walking on floors.

C. FUNCTIONS OF THE PREHENSILE TAIL. The tails of howler monkeys are always in use. During rest and sleep, the tail functions to anchor the animals to the branches of trees. After a young animal is about one month old it uses its tail to secure itself to its mother during rest as well as during locomotion, and this prehensile organ possibly accounts in part for the typical positions in which howler young are carried. The tail is used by resting animals to drive away flies and insects, and apparently as a currying or grooming organ, and I have seen both adult males and females manipulating their genitalia with the tip of the tail. During locomotion, this appendage functions as a grasping organ, and one which counteracts any tendency to fall. The tail is always carried in a position ready for immediate action (see plates 8, B, and 12, B). It would be impossible for an animal as large as a howler to feed in the manner that it does without a long prehensile tail.

The tails of monkeys vary greatly in degree of prehensiveness, and the howlers rank between capuchin and spider monkeys in this capacity. Capuchin monkeys have a semi-prehensile tail, whereas that of spider monkeys is extremely flexible and adaptive. The degree of prehensiveness is indicated by two things: (1) the proportion of the tail which is normally used for grasping, and (2) the arc through which the tail functions, if the point of attachment to the body is taken as a fulcrum about which the tail rotates. The grasping portion of howlers' tails roughly corresponds to the part of the tail which has a naked under skin. In an adult, this constitutes 20 cm., or about one quarter of the total length of the organ. The flexibility of the tail gradually decreases from the terminus of the naked part to where this appendage joins the body. The functional arc of the howler's tail is roughly 90° dorsally from the vertebral column and 120° ventrally. Howlers, during characteristic pronograde locomotion, use the tail most frequently in an arc described as about 10° above and about 15° below an extension of the spinal column. The lateral variation exhibited during locomotion is rarely more than an arc of 90°. Plates 7, A and B; 8, A and B; and 9, B, C, E, and F illustrate very well the longitudinal and, to a slight extent, the lateral arcs of function in howlers' tails. The prehensile tail is an organ of considerable importance in making possible the degree of arborealness found in howling monkeys.

D. Posturing. The posturing of howlers has considerable variability; hence it is difficult to describe typical postures. The following descriptions illustrate postures which are frequently to be observed:

1. Rather typical resting postures are those illustrated by plates 9, B, C, F and G. The animals are sitting with the rump and thighs in contact with the limb; the tails are tightly coiled around the branch; and the fore feet may or may not be in contact with

supports. From these postures, the animal may change to one of lying down with its head resting on its arms, hind feet dangling, and tail extended backward and coiled around the limb on which it is lying; or all four feet may be dropped as the animal straddles the limb and holds to it with its tail only. While resting, a howler may reverse the normal ventro-dorsal relation and lie on its back, grasping near-by branches with its extremities or merely holding on with its tail. A final variation commonly seen is that of an animal lying on either side and securing itself by using many possible combinations of grasping with the five appendages. A study of the illustrations will indicate some typical resting postures and their variations.

2. Feeding postures are illustrated by plates 7, A and B; 8, C and D; 9, H and I. Howlers usually move over the upper surfaces of branches to the terminal twigs and, while supporting themselves by their tails and hind legs, pull in with their hands the leaves, buds, or fruits which are then eaten directly from the stems. A howler may suspend itself entirely by its tail, as shown in plate 9, H and I, and feed in this position for as long as twelve or fifteen minutes.

The characteristic postures of primates affect the forms of all of their activities. In the following descriptions of locomotion, feeding, play, and other types of behavior, postures will be described or indicated.

E. Locomotion. The locomotion of howling monkeys is typically of the pronograde type. The spinal column is arched slightly, but the longitudinal axis of the body moves parallel to the support over which the animal is moving, whether it be an inclined limb, a perpendicular tree trunk, or a swinging vine. A howler on a horizontal branch places the forepaws on the limb, which is grasped between the first and second digits, the feet grasp the limb with the fingers opposing the great toe, and the tail is carried ready for grasping or actually does grasp the support intermittently (see plates 8, A and B; 10, E and F; and 13, A).

Howlers do not make long jumps from one tree to another, as do capuchins and spider monkeys. They select routes through the forest over which they can move by passing from the terminal branches of one tree to the terminal branches of another tree without making long jumps necessary. Jumps over spaces of ten or twelve feet are sometimes made, but always with extreme "caution." Young howlers which are independent during locomotion make longer and more frequent jumps than do the large adult animals.

The following observations describe both typical and atypical forms of howler locomotion:

Observation 5, Jan. 26, 1932, Group 1. Howlers used both hands, both feet, and the tail during locomotion. The movement was parallel and usually above the support over which they traveled. Only when they crossed from one limb to another did I see them swing on their arms, a suggestion of brachiating locomotion. Locomotion was slow and very "deliberate" in quality. Jumps of four or five feet were made after much hesitation.

Observation 6, Jan. 20, 1932, Group 1. An adult male moved along the under surface of a limb. His four feet and tail were employed for grasping and his movements were not uniformly forward, but he moved in a series of jumps. This is an example of pronograde locomotion with a reversal of the ventro-dorsal axis. In the same situation, a spider monkey would have displayed brachiating activity.

Observation 7, Jan. 6, 1932, Group 1. An adult male climbed a vine which hung perpendicular to the ground. He climbed in a hand over hand manner, walked with his rear feet, and held his tail in position ready for an immediate grasp of the vine.

1. Degree of arborealness. Howlers are strictly arboreal in the habitats in which I have observed them. They show a type of locomotion which is well adapted to an arboreal habitat. Whereas they are awkward and poorly coördinated in their locomotor patterns on the ground, activity which I have observed in captive specimens, they are much more nicely adapted to the oval surfaces of trees and vines. Only once did I see howlers on or near the the ground in the wild. This is reported in the following observation:

Observation 8, Mar. 27, 1933, Coiba Island. I was threading my way through extremely dense underbrush and between the banks of a small stream, when I heard a noise to my right. Animals were moving ten yards away and I hurried to the site. I discovered a small group of howlers which appeared to be just leaving the ground; they were in some bushes at that time about ten feet from a bank of the stream. They seemed frustrated by my approach and I came unusually near them.

Terrestrial locomotion is certainly not the normal mode of travel for howlers. H. C. Clark, of Gorgas Memorial Institute, who is well acquainted with Central American animals, reports having seen the howlers in sparsely wooded regions of Honduras passing from one clump of trees to another on the ground. There are reports current among natives, also, that howlers sometimes come to the ground and move from one forest or group of trees to another.

Howlers can swim when forced to do so. I placed a young adult female howler on a small island near the dock at Barro Colorado Island. The small island was separated from the larger one by about ten feet of water, and in addition there was a space of forty feet or more of dense, tangled marsh grass. Within three hours after release on the small island the monkey escaped to the large island. No trace of her having passed through the marsh grass was found; hence she must have swum at least fifty feet.

"Mexico," a dependable native, told me of having seen howlers swim across the upper Chagres River, and "Sylvestri," another unusually keen native observer, told a similar story. Both men had seen single and, according to them, male howlers swimming the river. These natives described the swimming as "mismo un hombre"—like a man, and demonstrated the movements of the arms as being those of overhand strokes.

2. Adaptive behavior during locomotion. Howler monkeys, when traveling through the average forest, adapt themselves to relatively stable objects. At times, however, it becomes necessary for them to adjust their locomotor activity to variable,

moving supports and at such times interesting behavior occurs which may throw light on their adaptive capacities.

Observation 9, Feb. 5, 1933, Group 1. Group 1 was moving from a large tree into a slender sapling, and from there into another tree. The trade wind was blowing strongly and caused the small tree to move back and forth. As it was blown toward tree no. 1 where the animals were located, one or more of the monkeys would cross quickly to the sapling, and as it moved near to tree no. 2, the animal would quickly dismount. All classes of animals down to small juveniles crossed without difficulty by timing their activity with the movement of the swaying tree.

The adaptation to a swaying tree is similar to the activity of adjusting to wind-blown branches or those set in motion by other passing animals. An individual may watch a branch intently for minutes until it is blown near enough to be reached, and then it is used as a means by which to travel to the next possible support in the line of progress. I have seen a young animal wait until adults had pulled together two opposing branches, and then while they were close together it crossed hurriedly.

Howlers also use vines and flexible limbs as levers and swings for crossing spaces too wide for them to cross otherwise. An individual may mount a swinging vine or limb, set it in motion by swaying back and forth, and eventually increase the oscillations until they are sufficient to carry the animal to the desired support. The use of objects as conveyors is a rather infrequent occurrence with howlers, but the activity illustrates a certain capacity to coördinate their movements temporally and spatially with changing supports. Possibly one could class this activity along with the use of objects which serve defensive purposes as a primitive type of instrumentation.

3. Rate of locomotion. Relative either to capuchin or spider monkeys, howlers travel slowly and for short distances at a time. It is difficult to determine the average rate of locomotion of individual howlers under normal conditions because they move in groups; therefore the rate of locomotion for an individual is the same as the rate of progression of the entire group. Individual males living temporarily alone are very erratic in their locomotion.

I estimate the rate of locomotion to be about the same as that of a man walking at a moderately rapid gait. Howler groups move in spurts and for short distances of twenty-five or thirty yards at a time. Group progression occurs at the rate of about one hundred yards per hour on the average, and rarely does a clan move more than five-hundred yards during a day (see figure 1, p. 44).

F. Feeding activity. The juveniles and adult howlers are herbivorous and frugivorous. Young buds, leaves, and fruits in varying quantities compose their diet. One needs only to contrast the feeding activities and food preferences of capuchins and howling monkeys to be convinced that specific food preferences exist.

1. Development of feeding in the young. Soon after birth, and before it is dry, the new-born howler finds the nipples, with the help of the mother, and it may be observed sucking at frequent intervals thereafter. While the infant is still being carried on the mother's belly, it begins to supplement its milk diet with solid food. The fecal matter of two infants captured when between two and three weeks of age showed that they had been eating hulls of almendro nuts at that early age. During this period, infants take partially eaten food from the hands of their mothers and nibble at it. Solid foods are eaten more and more frequently and they supplement the milk diet from this period until the young animal is weaned.

2. Feeding activity of adults. Howlers in the wild feed periodically or rhythmically. When there is an abundance of food only about one quarter of the daylight hours is spent in feeding. If the animals have passed the night where there is food, some random feeding may begin shortly after dawn; otherwise feeding follows a period of progression which rarely begins before seven o'clock and may be delayed until two hours later. Therefore as a usual thing, it is during the mid-part of the forenoon that active group feeding occurs. For a couple of hours almost the entire group may be engaged in continuous, active feeding. One by one the individuals of the group become satiated; the young ones begin playing; the adults become quiet and rest or sleep. Another period of progression may, but usually does not, follow

the morning feeding. Almost invariably there ensues a period of rest and inactivity. This period usually falls between 11 and 2 o'clock, depending upon the time of beginning and amount of activity engaged in during the morning. After the noon period of rest and sleep, the animals may move to another food tree or resume feeding where they are. Another period of two or three hours of active general feeding may occur during the afternoon, usually between two and six o'clock. Then the group moves to a lodge tree for the night, settling down between six and seven o'clock and remaining inactive until the next morning.

The following notes are of interest in connection with feeding activity:

Observation 10, Feb. 21, 1932, Group 1. Group 1 has remained for the past three days within the bounds of three trees. They have fed from a large fig tree, and they have rested and passed the night about 15 yards away in a tall espavé which was strangled by the matapalo fig. The animals as a group, as subgroups, or as individuals, moved back and forth between these loci according to the dominance of motivation. The nights were always spent in the espavé tree.

Observation 11, Jan. 31, 1932, Group 4. I have observed Group 4 regularly for several days. The animals have alternated between a preferred food tree and a lodge tree about 200 yards away. Invariably, the group has travelled from the lodge tree to the food tree in the early forenoon and back again in the late afternoon. It has moved roughly over the same route, which is the shortest distance between the two places.

I have tried to describe a typical diurnal cycle of feeding activity, but the changes of behavior are by no means regular. A group may feed intensively in a limited area for several hours, moving about very little, and then travel for half a day with only random feeding.

Feeding is facilitated or retarded by the behavior of associated animals. If an animal is forced to select between continuing feeding and following its group, it will usually follow the group. Feeding activity may cease at once if a clan is approached by another, by a complemental male, or by an observer. Were conditions such as to bring about keen competition for food, social facilitation and inhibition of feeding would be more prominent than it is in the communal groups of howlers.

a. Patterns of feeding behavior. Howlers feed directly from the terminal twigs or fruit stems of trees. The animal may feed from beneath or above the branch on which the food is found, or it may suspend itself by the tail from one collateral branch to within reach of food at a lower level, as shown by plates 7, A and B and 8, C and D. Usually the food is eaten directly from the stems after they have been pulled in, although at times twigs, leaves, or fruits may be plucked and eaten. Howlers do not usually take food in the hands before eating nor pick food and carry it away to be eaten.

Howlers are very wasteful of food. I believe it a conservative estimate to say that they drop and waste about one third as many leaves and fruits as they eat. One bite may be taken from a large leaf or fruit and the rest dropped. This wastefulness may relate to the lack of fine motor coördination in manipulation. Fruits or buds when pulled seem to become immediately a weaker incentive than those attached to stems; hence the plucked food is dropped and other near-by and attached foods eaten.

b. Sham feeding. A most interesting type of behavior has been observed in two situations: (1) The observer is quiet and partially concealed; a howler behaves as if seeking to get a better perspective by approaching nearer to the observer; it may casually pluck leaves and eat them as it approaches, (2) an animal may approach another and begin feeding, continuing to eat casually until within striking distance of the animal approached; then it may spring on the second individual and begin playing. I have observed similar sham feeding as the clan males approached a solitary male. The sham feeding would seem to be a kind of camouflage for the true quality of the behavior. The animal overtly displays a different form of behavior from that which would have occurred with the dominant motivation, and thereby gains advantages of time, nearness, or position.

c. Kinds of food. In order to learn what kinds of food howlers eat, I collected specimens of the leaves and fruits eaten by them from January to May, 1932. These specimens were sent to Paul C. Standley of the Field Museum in Chicago for indentification. Standley is an authority on Central American flora (58). Other specimens were identified in the field from their native names.

Araceae

A vine. Leaves eaten and possibly the flowers. Of minor importance.

Moraceae

Coussapoa panamensis Pittier.

Ficus Colubrinae Standl. A small tree whose fruit is eaten.

Ficus costaricana (Liebm.) Miq. A large tree. Leaves and fruit are eaten, and when the fruit is ripe this tree may supply the principal part of the howlers' diet. The fruit resembles figs which are cultivated. This tree is known to the natives as "Matapalo," "Higo," or "Higuero."

Ficus crassiuscula Warb. An important food tree, the fruit of which is eaten.

Ficus glabrata HBK. Higuerón. The very large fruit of this tree is eaten. It is dry and sweetish with many seeds. This fruit and other species of *Ficus* may contain worms which are eaten by the monkeys with the fruit, thus indirectly providing a protein food. This tree is one of the most important sources of food.

Ficus Oerstediana Miq. A tree bearing small fruit and leaves which are eaten.

Ficus Tonduzii Standl. A common Ficus whose leaves and fruit are eaten.

Helicostylis latifolia Pittier. A tree which grows a kind of nut covered with a thick green hull. It is called "Berba" by the natives and there is a closely related species which is called "Berbacilla." During June and July the fruit of Berba is second only to figs in importance as food for most of the animals of the forest. The red spider monkeys in the Coto region feed principally on Berba, Berbacilla, and Bogamani in June and July.

Annonaceae

Guatteria amplifolia Triana and Planch. A small tree whose leaves, flowers, and berries are eaten.

Guatteria dolichopoda Donn. Smith. A tall tree whose leaves and berries are eaten.

Myristicaceae

Virola panamensis (Hemsl.) Warb. A tree known as Bogamani or Wild Nutmeg. Howlers eat the leaves to some extent and the inner hull or aril of the nuts.

Caesalpinieae

Parioria copaifera Griseb. Cativo. A tall forest tree from which howlers eat leaves and the unripe seed pods.

Papilionatae

Diphysa robinioides Benth. Macano, Cacique. This tree flowers about the middle of the dry season and howlers eat the bright yellow blossoms and leaf buds.

Dipteryx panamensis (Pittier) Hubbard & Rehder. Almendro. This nut-bearing tree supplied between one third and one half of the food eaten by howlers during the last of January and February, 1933. The previous year, the trees bore very few nuts. The meaty, sweet and juicy hulls of the nuts as well as the leaf buds are eaten.

Platymiscium polystachyum Benth. Quira. A large forest tree of which howlers eat the leaves and flowers.

Platypodium Maxonianum Pittier. Carcuera. A tall tree of which leaves, flowers, and fruit are eaten.

Pterocarpus Hayesii Benth. Bloodwood.

Rutaceae

Zanthoxylum panamense P. Wilson. Arcabú, Acabú. A tree whose leaves and buds are eaten.

Simaroubaceae

Simarouba glauca DC. Aceituno. Leaves and fruit of this tree are eaten.

Burseraceae

Protium asperum Standl. Howlers eat the leaves of this tree, but it is not very frequently found in the forest.

Protium panamense (Rose) I. M. Johnston Cope. A large tree from which the leaves are eaten.

Tetragastris panamensis (Engler) Kuntze. Fruit and leaves of this tree are eaten.

Meliaceae

Guarea guara (Jacq.) P. Wilson. Cedro Macho. Howlers sometimes feed from this tree.

Malpighiaceae

Stigmaphyllon Humboldtianum Juss. The leaves and flowers of this vine are taken in small quantities.

Euphorbiaceae

Hieronyma alchorneoides Allem. Pantano. A tall forest tree of which buds and fruit are eaten.

Anacardiaceae

Anacardium excelsum (Bert. & Balb.) Skeels. Espavé. Due to the frequency of occurrence of this tree and the abundance of leaves and beans which it produces, espavé is one of the most important trees in the howlers' habitat.

The buds and leaves are eaten in December and January and the beans several months later.

Spondias Mombin L. Hogplum; Jobo. The leaves are eaten.

Sapindaceae

Paullinia Baileyi. The leaves of this tree are eaten.

Tiliaceae

Apeiba aspera Aubl. A medium sized tree whose leaves are infrequently eaten.

Apeiba tibourbou Aubl. Peine de Mico ("monkey-comb").

Belotia panamensis Pittier. The leaves of this tree are eaten.

Bombacaceae

Bombacopsis Fendleri (Seem.) Pittier. Cedro Espinoso. The buds, leaves, and flowers of this tree are eaten.

Bombax barrigon (Seem.) Dcne. Barrigón. The flowers of this conspicuous tree are eaten in small quantities.

Cavanillesia platanifolia HBK. Cuipo, Bongo, Quipo. I have observed howlers feeding for short intervals on the flowers of this tree.

Marcgraviaceae

Souroubea guianensis Aubl. The leaves and roots of this epiphytic plant are eaten.

Guttiferae

Calophyllum longifolium Willd. María. From this tall forest tree, I have frequently seen howlers feed on the leaves, but I have not found evidence of their eating the fruit which it bears.

Clusia odorata Seem. Copey. Howlers eat the flowers and fruit of this glabrous tree.

Rheedia madruno (HBK.) Planch. & Triana. Madroño, Fruta de mono (monkey fruit) Machari.

Lecythidaceae

Gustavia superba (HBK.) Berg. Membrillo. Flowers and fruit are eaten.

Combretaceae

Terminalia Hayesii Pittier. Amarillo real.

Myrtaceae

Psidium Guajava L. Guava; Guayaba.

Araliaceae

Didymopanax morototoni (Aubl.) Dcne. & Planch. Mangabé, Gargorán, Pava. A large tree from which howlers frequently feed, eating young leaves and buds.

Myrsinaceae

Ardisia compressa HBK. A glabrous tree from which the flowers and fruits are eaten.

Stylogyne ramiflora (Oerst.) Mez.

Sapotaceae

Chrysophyllum Cainito L. Star-apple; Cainito. A common forest tree which bears leaves and fruit eaten by howlers.

Apocynaceae

Aspidosperma megalocarpon Muell. Arg. Leaves and probably flowers are eaten.

Stemmadenia grandiflora (Jacq.) Woodson.

Verbenaceae

Petraea volubilis Jacq. Viuda, Flor de Mayo, Flor de la cruz. The conspicuous flower of this vine is very frequently eaten.

Solanaceae

Markea panamensis Standl. An epiphytic vine.

Bignoniaceae

Arrabidaea pachycalyx Sprague. The leaves and possibly the flowers of this vine form part of the howlers' diet.

Tabebuia guayacan (Seem.) Hemsl. Guayacán. Howlers eat the flowers and possibly the leaves of this tree.

Tabebuia pentaphylla (L.) Hemsl. Roble, Roble de sabana. Howlers feed from this tree while it is in flower and after the leaf buds appear.

Rubiaceae

Alibertia edulis (L. Rich.) A. Rich. Lagartillo, Trompito.

Genipa americana L. Jagua.

Psychotria racemosa (Aubl.) Willd.

This list is only partially complete, but it contains the major kinds of foods eaten during the months when the study was made, and shows the wide range of kinds of trees from which howlers feed.

At times, animals leave a tree filled with food and move over to another one of a different kind. Many ripe figs may be left for an almendro tree, or either of these may be left and the animals move to a distant espavé to feed on the buds or the beans. Howlers show definite food preferences, but they are not as specialized in their food habits as capuchin or spider monkeys.

I do not know what foods the animals eat from June to December. I infer that after the beginning of the rainy season, just as during the first part of the dry season, buds and young leaves are very plentiful as the new crop of vegetation grows. Apparently throughout the year in the tropical forests of Barro Colorado Island there is a constant succession of budding, flowering, and fruiting trees. The periods when food is most scarce are, I believe, the last part of the wet season, November and December, and the last part of the dry season, April and May. Even then, during the latter period howlers are well-fed. Being leaf eaters as well as fruit eaters, their food supply does not fluctuate like that of the spider monkeys, which are primarily fruit eaters. I believe that on Barro Colorado Island with its present population of howlers there is no season when there is a scarcity of food.

Howlers consume large quantities of food which is bulky and fibrous. I have removed as much as three pounds of mash from the stomachs of adult howlers, and relatively large amounts of mash from younger animals. They take many times the amount of bulky, fibrous foods eaten by spider monkeys of a comparable size.

Howling monkeys evidently obtain necessary water from two sources. The most important of these is the water content of leaves and fruits which may be 95 per cent of some foods by weight. I have observed animals many times either licking water directly from leaves or limbs as it collected there during a downpour of rain, or first wetting their fingers on the dripping limb and then licking the water from them. I have only very slight evidence to indicate that howlers ever come to the ground to drink from streams of water (see observation 8, p. 33). Necessary water apparently is obtained from the two sources listed above.

G. SUMMARY. In this section I have shown that howlers have a concentric type of prehension with a functional division of the hand between the first and second fingers; the thumb is non-opposable, and in grasping the fingers move concentrically toward the palm. The feet and prehensile tail have been described and criteria suggested for determining the degree of prehension of the tail. Typical postures and many variations were described.

The locomotion of howlers is of the pronograde type, with few variations of any kind toward orthogradeness. Instances of adaptive behavior during locomotion were cited. Howlers are almost entirely arboreal. When necessary, they can swim. The feeding activity of howlers was described and a list given of the leaves, flowers, and fruits which they eat. Howlers apparently secure water, in the main, from the foods they eat, but also from rain-water which collects on leaves and limbs.

VI. TERRITORIALITY AND NOMADISM

In a systematic study of the social behavior and groupings of primates it is important to know whether or not groups or individuals adapt themselves to definite territories. The adaptation of several groups or many individuals to a common territory may result either in frequent close spatial association or in frequent conflict and competition. If animals do not adapt to particular home areas but are strictly nomadic, it is desirable to know the determinants and characteristics of their wanderings. If they are restricted to limited areas, the movements of clans or individuals within this area demand study.

Answers were sought to the following questions relative to the territoriality and nomadism of howling monkeys: What types of habitat are preferred? Do howling monkeys have specific territories or are they strictly nomadic? What factors limit the range of groups if they do have definite territories? What are the relations between group size, amount of available food, and extent of territorial range?

The territorial range of a group of animals may be determined either by following the group continuously for a time or by identifying it repeatedly in relation to specific locations. It is possible to follow the movements of a howler clan because of the characteristic daily rhythms of activity, the relatively slow progression, and the short distances covered. It is also possible to identify repeatedly some groups with considerable certainty. Groups may be identified by the number and kind of animals which they contain and by individuals which can be differentiated. If we assume that groups are relatively stable societies, these factors make it

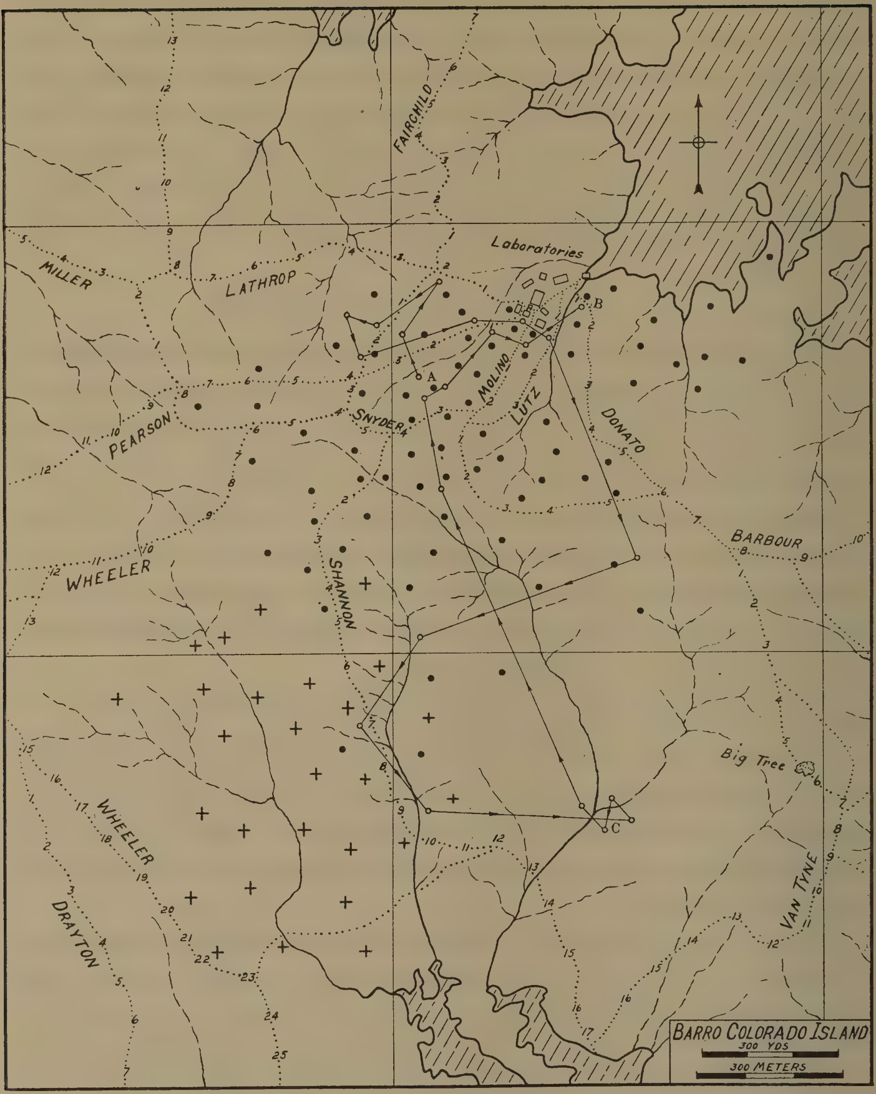
Laboratories
FAIRCHILD
MILLER
LATHROP
PEARSON
SNYDER
MOLINO
LUTZ
DONATO
A
B
C
BARBOUR
WHEELER
SHANNON
Big Tree
WHEELER
DRAYTON
VAN TYNE
BARRO COLORADO ISLAND
300 YDS
300 METERS

Fig. 1. Drawing of a Section of Barro Colorado Island

Dots and crosses indicate where Groups 1 and 2 respectively were located in 1932. The lines and circles show the direction and distance of movement of Group 1 during twenty-two consecutive days in January, 1933. (Drawing by P. E. Nelbach.)

possible to ascertain the characteristics of group movements and their territorial range.

A. TERRITORIAL RANGE OF GROUP 1. The month of January, 1932, was spent in making daily observations on Group 1, a clan which ranged near the Laboratory on Barro Colorado Island. The group was followed and observed during the day, left at night, and observations continued the following morning. At this time, the group contained a total of twenty-six animals. There were three males, seven females without infants, four mothers carrying infants, and eight juveniles.

Each time that the group was positively identified as Group 1, its location was plotted on a map. The dots on figure 1 indicate the approximate locations where the clan was identified. Group 1 was located and identified seventy-three times during the month of intensive study and during the following four months. It was believed that this sampling of the places where Group 1 was located would delimit the territory of the group. A boundary including all of the plotted points would roughly include the territory of the group, provided the number of locations was sufficient and covered a sufficiently long period of time. A line which includes all of the plotted points would begin at the Laboratory, run to Barbara Lathrop 3, to Pearson 8, to Shannon 9, to Barbour 8, almost due north to the lake and thence back to the Laboratory. The area included is roughly circular and has a radius of slightly over six hundred yards. The focus of the area, that is, the place where the group was found most frequently, lies along Snyder-Molino near the origins of Shannon and Barbour Trails.

I followed the consecutive daily movements of the clan which I found in the same region surrounding the Laboratory in January of the next year. Because of the comparable constitution of the group and the presence of recognizable individuals, I am reasonably sure that the clan was the Group 1 which I had studied intensively the previous year. Beginning at point A on the accompanying map, figure 1, I have plotted the daily movements of the clan for twenty-two consecutive days. The straight line and arrows indicate the approximate direction and distance of movement and the circles indicate the places where the nights were spent. During the twenty-two days, the clan ranged from Lathrop 2 to near Shannon 13, from Shannon 7 toward Van Tyne 13 and then to near Barbour 6, and from near Donato 0 to Pearson 4. The limits of these movements extend beyond the limits established the previous season only in the region toward Van Tyne Trail.

The group traveled from about fifty yards to about eight hundred yards per day (see figure 1). The average distance covered was approximately two hundred yards per day. The long distances were usually covered in several periods of movement during the day. At times, as at location C, the group fed for three consecutive days from the same almendro tree. Following this relatively stationary feeding, the group began moving and travelled approximately eight hundred yards; this type of activity has been noted many times. The behavior of the clan at C is an example of limited group movements due to concentrated food supply. When the clan returned to point B, three consecutive nights were spent in the same lodge tree. Each day the clan would move away from the lodge tree, feed, and then return at night. The direction of the movements of the clan in relation to the focus of the territory is worthy of note. As a group approaches the limit of its range, its course changes and it moves back toward the focus of its area. At Shannon 7 the course of Group 1 was deflected by a vocal battle with Group 2. At point C there is a rather sharp transition from primary to scrub forest. These are examples of situations which deflect the direction of group progression.

Summarizing from these data, it may be said: (1) that Group 1 with between twenty-five and thirty animals has a territorial range of approximately three hundred acres; (2) that intermittently during more than eight months, included in two different dry seasons, Group 1 was identified in this area; (3) that, with the exception of the area along Shannon from 4 to 13, no other clan of howlers was found in this territory, although foreign individual males were at times seen here; and (4) that the movements of the group within the area are rather restricted and occur with reference to food and lodge trees.

B. The range of group 2. During the two seasons of work

Group 2 was definitely identified twenty-six times, as shown by the crosses on figure 1. The limits of the range of this group are even more restricted than that of Group 1, yet the two clans are of approximately the same size. The less extensive range of Group 2 is related to the extremely dense, tall forests which cover the region between Shannon and Wheeler Trails. Here there is a concentration of food as well as preferred lodge trees.

The territorial range of a group is not accurately represented by the square area which it covers. The altitudinal forest range must also be taken into account. Of two groups, the one living in an extremely dense, tall forest, the other in less dense and lower forest, the latter, other factors being equal, will have the greater lateral range. The territory of arboreal animals should be considered as being three dimensional.

The overlapping region of the territories of Groups 1 and 2 lies along Shannon Trail from 4 to 13. In this region the two groups were in frequent conflict as evidenced by vocal battles between them (see inter-group relations, p. 115).

C. THE LOCATION OF OTHER GROUPS. I attempted to apply, in part, the procedures followed in studying the ranges of Groups 1 and 2 to other groups of the island during the months from February to May, 1932. Group 3 was located and identified 4 times as shown on figure 2, pp. 48–49. Group 4 was located six times, Group 5 six times, Group 6 fifteen times, Group 7 fourteen times, Group 8 seven times, Group 9 five times, and so on as may be noted on the map for the remaining groups. Figure 2 indicates the ranges of Groups 1 and 2 as shown by the boundaries of dots. The numbers indicate general location and suggest the ranges of the other twenty-one groups during the time that they were being studied.

The different groups were re-identified and located after periods of time varying from a day to several months. Furthermore, I am reasonably sure, judging from the group constitution as well as a few identifiable animals, that Groups 1, 2, 4, 5, 6, 8, 9, 21, and 22 were found in the same general regions in 1933 that they occupied in 1932. On the other hand, some groups were not located in the territories of the previous year. Groups 12, 15, and 23 could not be found in 1933 in areas of the island which they occupied in 1932.

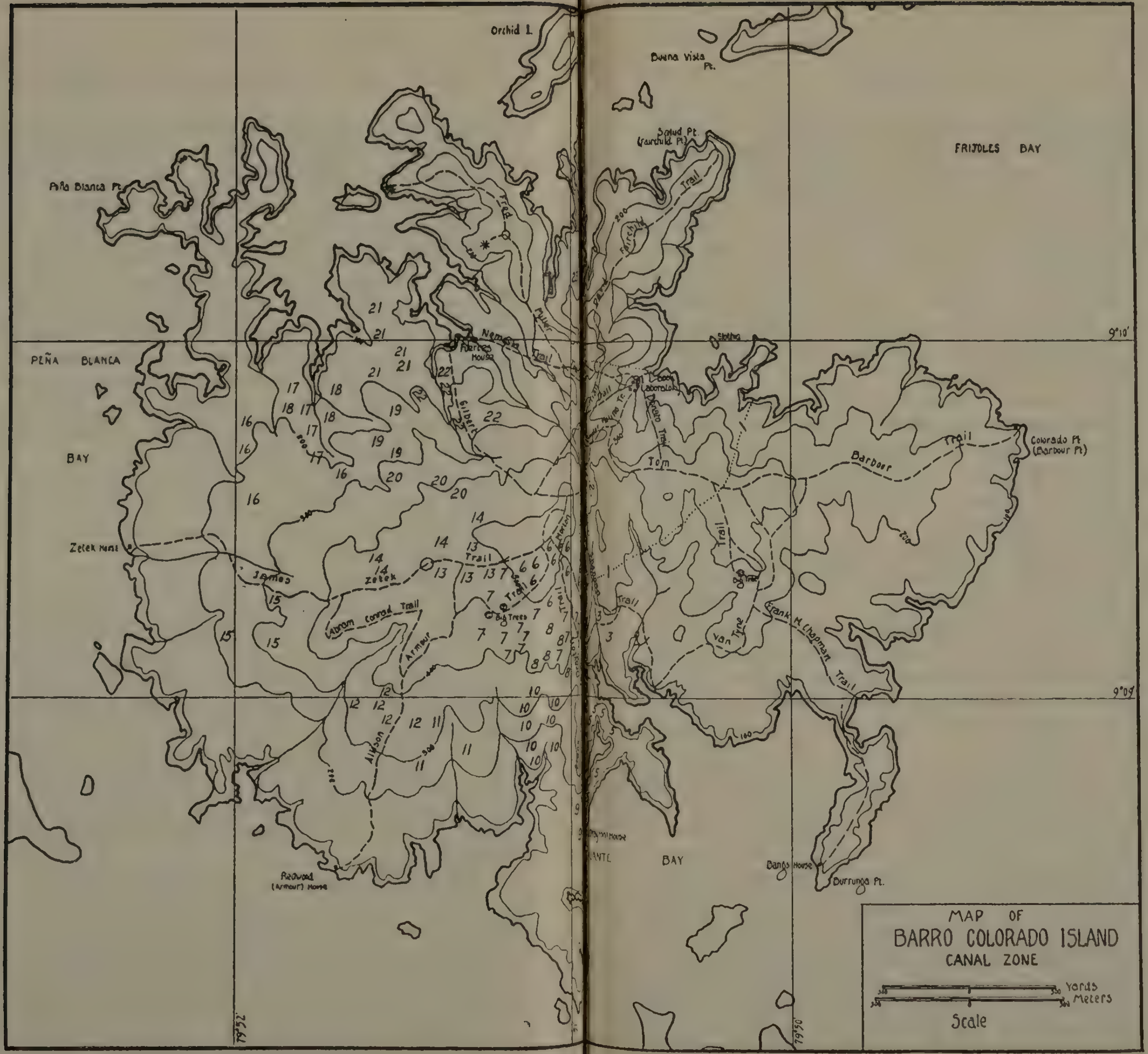
Orchid I.
Buena Vista Pt.
Salud Pt. (Fairchild Pt.)
FRIJOLES BAY
Peña Blanca Pt.
PEÑA BLANCA
BAY
Forbes House
Nemesia Trail
Laboratory
Fairchild Trail
Wheeler Trail
Gilbert Tr.
Barbour Trail
Colorado Pt. (Barbour Pt.)
Tom Trail
Zetek House
James
Zetek Trail
Abram Conrad Trail
Armour
Big Trees
Van Tyne
Frank M. Chapman Trail
Allison
Redwood (Armour) House
BAY
Bangs House
Burrunga Pt.
9°10'
9°09'
79°52'
79°51'
79°50'
MAP OF
BARRO COLORADO ISLAND
CANAL ZONE
Yards
Meters
Scale

FIG. 2. A CONTOUR MAP OF BARRO COLO HOWING ITS FORM, TRAILS, AND HOUSES

The figures indicate where each of twenty-three groups of howlers was locat etition of a figure shows where, and the number of times, a group was checked. (Drawing by courtesy of The Arnold Arboretum of Harvard University.)

It seems probable that from year to year there is a gradual shifting in the territorial ranges of some clans. As clans increase in size, their range may be extended. A clan may be crowded out of a particular area or ravine by the encroachment of another clan, and when new clans are formed they may come to inhabit areas at least partially new and different from the range of the parent clan. Depending on the presence of food and preferred lodge trees, a clan may exclusively employ or entirely neglect certain regions during one season which are used during another year. Thus it is seen that the possession of territory is not a static but a dynamic adaptation.

It is clear from the study of the locations of the clans of howlers that there is considerable overlapping of the territories of some groups, and that the ranges of several groups may be almost identical, that some groups are relatively isolated, and finally that the shifting and extending of territorial ranges are constantly occurring with particular groups.

D. Nomadism of howler clans. Animals are said to be nomadic if they wander continuously without reference to a fixed abode. Heape (35) has pointed out that this definition does not accurately describe the movements of most animals because they usually have home areas. Howling monkeys are not strictly nomadic because clans of these animals show strong tendencies to limit their wandering to a definite area, and because within the home area movements may occur relative to abode or food trees for several days at a time.

There are within the indigenous territory of a group at any given time many preferred food and lodge trees. There are also places where the clans loiter and rest. These function as foci of activity, i.e., as goals. There is a network of pathways connecting the goals and sub-goals. Apparently as the group moves over certain pathways which lead to preferred goals, the activity is facilitated and the pathway is learned. The location of food and lodge trees as well as prominent arboreal routes within the territory of a group are learned and become positively attractive to the animals. When a clan moves toward the border of its territory and the pathways and goals become less and less well-known, there is much frustration, progression is slowed, and the group becomes re-oriented toward the more familiar pathways and better known goals.

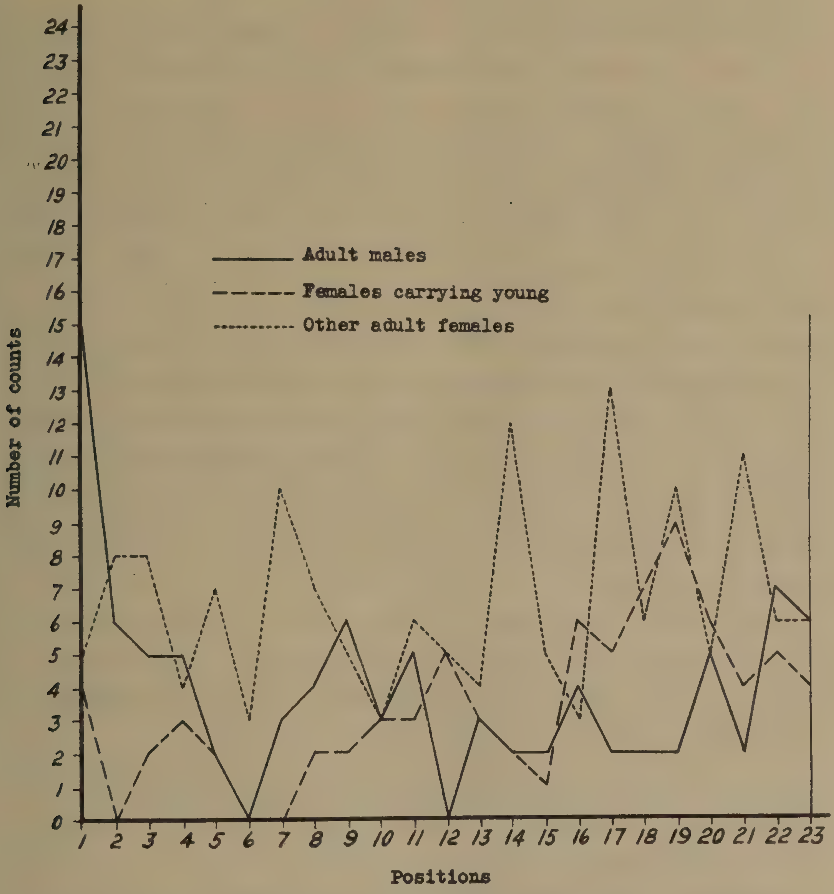

FIG. 3. SHOWING THE DISTRIBUTION OF THREE CATEGORIES OF HOWLERS IN 23 POSITIONS FOR 24 DETERMINATIONS

1. The form of grouping during progression. Howler groups have the form of an irregular column of moving animals during progression. At critical crossings such as that shown in plate 8, A and B, all animals in a clan may cross one after another over the same limbs. Furthermore, animals of particular categories have tendencies to move in certain positions in the line of march.

In order to learn what positions in the column of animals the males (M), adult females carrying babies (m), adult females without babies (f), and young (i's and j's) tend to assume during progression, I made 24 counts on Group 1. The animals were classified and listed in the order of their crossing in single file from one tree to another. The accompanying graph, figure 3, shows the results of this study of the order of group progression for three classes of animals. In position 1, i.e. the first animal to make the crossing, adult males were found fifteen times out of twenty-four counts. At other times one or more males were in the first three to five positions. Females carrying young and those without babies were found four and five times respectively in position no. 1. The curve for the males shows three modes, but there is a strong tendency for the males to move in the forward and last positions. I could identify two of the four males in this group and my records show that no particular male tended to assume a definite position. Male "No. 1" or male "M.r." (the r indicates his distinctive reddish coloring) were sometimes found in the first position and at other times in the last position, or in intermediate positions. The tendency is for any one of the four males to be in the first few forward positions.

The curve for the mothers is also tri-modal, but there is a tendency for mothers to travel in the last positions of the column of animals. There is no marked tendency for either females or young animals to move in characteristic positions.

The following are examples of the records of the order shown during a crossing (see p. 58 for description of symbols):

Example 1: M, f, j3, f, j3, j3, M, f, m/1, 5, M "No. 1," j1, j2, j2, j3, m/1, f, m/2, m/2, j3, j1, f, "M.r."

Example 2: M "No. 1," j3, f, j1, f, j1, j2, m/2, M, f, j2, j1, M, M, f, j2, j3, j3, f, j3, m/2, m/2, m/2, "M.r."

The following observations are pertinent:

Observation 12, Apr. 11, 1932, Groups 2 and 16. In Groups 2 and 16 today, I observed females in the foremost positions. Even so, these animals behaved with reference to a male which followed them closely. The males very definitely controlled the rate of progression, for when they stopped, the entire clan stopped.

Observation 13, Apr. 14, 1932, Group 1. Most of the animals of Group 1 had moved out of the tree in which they had been resting and were traveling toward a lodge tree. Three males and several females did not follow, but began progression in the opposite direction. One of the males began clucking, and the animals which first left the tree, reversed their course and joined the male leaders.

Observation 14, Apr. 12, 1933, Group 4. Today I checked on the order of progression of Group 4 and the results showed an extreme of the ordering tendency which is normally shown. The order of progression as observed follows: *M*, *M*, j3, j3, M, f, j2, f, j1, m/2, f, m/3, m/3, m/2, m/3.

These data characterize the form and order of howler group progression. They show the tendency for the males as a group but not specific individuals to control or lead the clans of animals.

E. THE PREFERENCE OF HOWLERS FOR PRIMARY FORESTS. Groups of howlers are also restricted to their indigenous areas because of situations at the borders of their territories which they tend to avoid. Howlers tend to avoid scrub forest of low altitude. When a clan comes into a region of scrub growth it usually reverses its course toward the dense, tall primary forest which is the familiar habitat.

The twenty-three groups of howlers observed in 1932 and the twenty-eight groups observed in 1933 were all found in what is called the primary forest of the island. In this forest there seems always to be an abundance of food. At times, however, there is also plenty of food in the scrub forest, yet one rarely finds howling monkeys in these latter regions. The question arises as to why howlers are found in the main in dense primary forest.

In primary forest the food supply is more uniform than in scrub areas. During the first part of May, 1933, howlers had withdrawn from certain areas on the west side of the island. The vegetation of these regions was parched by the long dry season and hot sun. At the same time there was plenty of food and shade in the deeper forest. In dense forest there are continuous arboreal routes over which howlers may travel. This is not true of low growth. There howlers are frequently frustrated by coming to the end of a pathway. In scrub forest also there are many weak lateral branches which are not suited to the rather heavy howler with its pronograde type of locomotion and its inability to make long jumps. Conditions in the secondary or scrub forest, in relation to continuous food supply, adequate support, protection from sun and possibly wind, are such as to cause howlers to avoid this type of vegetation. On the other hand, conditions in the primary forest attract them and are well suited to meet their needs.

There is another consideration which may be of importance. Of two positions varying in height from the ground, other factors being equal, the higher one would be preferred by howlers. The howlers are attracted by lures which are upward and away from the ground. Apparently they avoid the ground. This attraction upward and avoidance of the ground may also, along with other factors, function to limit howling monkeys to high, primary forests.

Clans of howlers avoid each other. When groups come into close proximity, vocal battles occur. Also Groups 1 and 2 have at times behaved as if they were guarding their particular regions and driving the other clan away by persistent vocalization.

Some of the factors operating to limit the territorial range of groups of howlers are: (1) The conditioning of a clan to goals within the area and the acquired facility of reaching these goals over learned pathways. (2) The tendency to react positively to the familiar and to avoid the strange, interacting with a tendency to explore. (3) The tendency to avoid scrub growth or other unsuitable vegetation. (4) The tendency to avoid other clans. (5) A strong "preference" for primary forests.

E. Summary. In this section I have given data which indicate with considerable reliability the territorial range of one large group of howlers. Sufficient data were given to suggest the limits of the range of a second clan. Twenty-one other clans were located and identified repeatedly. It has been shown that howler groups travel within a rather limited area and that within this territory they are semi-nomadic. Howler groups characteristically travel in the form of an irregular column, and the males and females with babies are found respectively toward the fore and toward the rear of the moving column. Howlers show a definite preference for primary forest and apparently avoid scrub growth. Some reasons why this is true, as well as reasons for territorial adaptation, have been advanced.

VII. ORGANIZATION OF A HOWLER POPULATION

The investigation of simian social relations and behavior requires in the beginning an analysis of the way in which animals of a particular family, genus, or species are organized. It is desirable to determine the number and kind of animals which compose the groups, and the central tendencies and the variability of these groupings. Information on the degree of stability which characterize the groupings of particular families or genera is also important. After data on these subjects are available, an analysis may be begun of the intra- and inter-group relations.

A. SUITABILITY OF SUBJECTS AND PROCEDURES. The characteristics of howling monkeys, the behavior of groups, and the situation on Barro Colorado Island are favorable for the study of the howler population found there. Since the animals are arboreal and do not flee for long distances from an observer, the groups can be followed closely and observed. The individual and sex differences make it possible to classify the animals into a number of categories. The single file form of group progression aids in the reliable counting of the individuals in a group. These factors were advantageous in the making of two censuses of the howler population.

The procedure used in making the census was as follows: A clan was first located. This was done by following vocal cues, odor, food waste, excreta, and so forth or, if it was known that a group was located in a particular area, that area was searched until the group was found. Since howlers almost invariably roar at the break of dawn, it was possible to spot clans by these early morning howls. At times either I or my assistant would spend the night in the general region where we suspected a clan to be located, and then we would find it by the morning howls. After a clan was located, it was carefully observed and notes were made on the number and kinds of animals which it contained. This was not always sufficient, however, and usually it was necessary to wait in ambush until the clan began progression, and then as the group crossed in irregular single file from one tree to another, each animal was counted and classified. The process of determining the constitution of a group required at times several hours, at other times several days, depending upon the timidity and wildness of the animals and upon the type of trees in which they were located. After the preliminary study and the count and classification of the animals during progression of the group, a check count was made if that was at all possible.

Once a census was begun, it was continued by working in consecutive areas of the island until the count was completed. While studying Group 1, for example, Group 2 would probably give several howling roars which would serve as cues for its general localization. Likewise while I was making determinations on Group 2, vocal cues could usually be heard which would lead to the location of Group 3. If an adjacent group was not heard or otherwise located, the forest was thoroughly combed for any possible indication of the presence of a clan. In general, the clans were located in 1932 in the order of listing presented in figure 2, pp. 48–49.

B. THE TOTAL HOWLER POPULATION OF BARRO COLORADO ISLAND. In April, 1932, a census showed that there were 398 group-living howlers on the island. Estimating the probable error at 50 individuals, although it is more probable that groups were overlooked rather than counted twice, the total population figure may be expressed as 398 ± 50. In April of the following year, 489 group-living individuals were counted and classified. This census is believed to be more reliable and the total figure may be expressed as approximately 489 ± 25 individuals.

The howler population of Barro Colorado Island is apparently increasing rapidly. In 1933, 91 more individuals were observed than in 1932. According to my classification and counts, 65 infants were included in the 1933 census which were still carried by their mothers continuously during progression and which were probably less than one year of age. Comparisons of the frequency of howlers on the island and on the mainland of the Canal Zone further indicate that the number on the island is rapidly increasing. On the mainland the groups are very small and scattered. This condition contrasts sharply with the relatively large groups which are crowded together on the island. I believe a conservative estimate to be that the island's howler population is increasing at the rate of approximately 15 per cent per year.

The question arises as to when the population will reach its maximum and what this number will be. It is important to note that there are many areas of the island with adequate forest to support howlers, but no groups are found there at present. Growth of the secondary forest may provide a suitable habitat for additional groups. Possibly more than two thousand howlers could be supported by the forest of Barro Colorado Island.

The figures of the total population do not include the complemental or so-called "solitary" males. These are met with rather infrequently. While they are alone and not associated with a group, they are difficult to locate and it is impossible to determine with accuracy the total number on the island. I met five complemental males in 1932 and six in 1933. I believe that these animals do not constitute more than 3 per cent of the total population at any given time.

C. THE VARIABILITY OF GROUPS. The 398 ± 50 individuals observed in 1932 were found living in 23 groups, and the 489 ± 25 animals of 1933 were found in 28 discrete groups. The 23 groups of the first census ranged in size from 4 to 35 animals, and the 28 groups of the second census ranged in size from 4 to 29 individuals. The mean and standard deviation for groups of the first census were 17.3 ± 6.8. This is to be compared with 17.4 ± 6.8 for the second census. The median group for the second census contained 18 animals. The relatively great variability of group sizes, as shown by the range (see table 1), indicates the lack of a strong tendency in these animals to form groups of a uniform size and kind. It is significant, however, that groups smaller than 4 or larger than 35 were not found, for it would seem that there are forces operative to limit group sizes within this range.

D. GROUP CONSTITUTION. The individuals of the groups were classified as they were counted into nine categories: (1) Males (M); (2) females without infants (f); (3) females carrying infants (m) m/1, 2 or 3 indicates a mother and infant; (4) infants carried on the bellies of the mothers (i1); (5) infants carried on the mothers' backs (i2); (6) infants partially independent of their mothers (i3); and (7), (8), and (9) juveniles (j1, 2 & 3) of different size, color and degree of independence.

TABLE 1

Census of the howler population of Barro Colorado Island, April, 1932

GROUPS*	MALES	FEMALES	MOTHERS	INFANTS AND JUVENILES						TOTALS
				i1	i2	i3	j1	j2	j3	
1	1	3								4
2	1	2	1			1				5
3	1	2	2	1		2	1	1		10
4	2	3	2		1	1	2			11
5	2	3	3	1	1	1	1	1		13
6	3	5	2		1	1	1	1		14
7	2	3	3	1	2		1	1	1	14
8	2	3	3	2	1		1	2		14
9	4	4	1		1	1		3	1	15
10	3	4	2	1	1		2	1	1	15
11	2	2	4	2	1	1		2	1	15
12	4	6	2		2			2	2	18
13	2	5	3	1		4	2	1		18
14	2	5	3	1	1	1	2	2	1	18
15	3	7	2		2		3	1	1	19
16	2	5	3		2	2	1	3	1	19
17	4	6	4	2	1	1	1	1		20
18	3	5	3	1	1	1	4	2		20
19	4	4	2		1	2	2	5	2	22
20	1	5	5		1	6	1	3	2	24
21	6	10	3	1	2	1		1	3	27
22	4	7	5		4	1	3	4		28
23	5	9	5	1	1	3	2	5	4	35
Totals....	63	108	63	15	27	30	30	42	20	398

1. The clan males (M). The adult males of a clan have the following characteristics by which they may be distinguished: (1) The whitish scrotum (see plate 9, B); (2) the large size relative to adult females, accentuated by longer hair; (3) the beard which

gives the head a massive, square appearance (see plate 5, A); and (4) the characteristics of behavior, particularly of vocalizations, reaction to an observer, and the activity of leading the clan. The adult males of a clan can be differentiated by an experienced observer with high reliability.

TABLE 1—*Concluded*

Census of the howler population of Barro Colorado Island, April, 1933

GROUPS*	MALES	FEMALES	MOTHERS	INFANTS AND JUVENILES						TOTALS
				i1	i2	i3	j1	j2	j3	
1	1	1	1		1					4
2	2	2						1		5
3	2		2		1	1				6
4	2	4					1	1		8
5	1	1	3	1	1	1		2		10
6	1	2	2	1	1		2	2		11
7	2	4	2		1	1	1	1		12
8	3	4					3		3	13
9	2	2	3		2	1	1	2	1	14
10	2	2	4	1	1	2	1	2		15
11	2	2	3	1	1	1	1	2	2	15
12	3	1	5	1		4	2	1		17
13	3	5	3	1	2		1	2	1	18
14	3	2	5	1	1	3		2	1	18
15	3	3	4	2	2		2	3		19
16	3	3	4	1	2	1	1	2	2	19
17	4	8	2	2			2		2	20
18	3	4	5		2	3	2	1		20
19	3	1	5		5		3	3	1	21
20	3	6	3	1	2		2	3	1	21
21	4	4	4	1	3			3	4	23
22	3	3	5	1	1	3	1	4	2	23
23	4	5	4		3	1	2	3	2	24
24	5	2	7	1	5	1	1	3		25
25	5	5	6	2	3	1	1	1	1	25
26	5	10	3	1	1	1	3	2	1	27
27	3		9	1	3	5	2	2	2	27
28	5	8	4	1		3	2	3	3	29
Totals....	82	94	98	21	44	33	37	51	29	489

* Groups are here numbered in order of size. These numbers do not correspond to those in text or on the maps.

There were 63 adult males in the 23 groups of 1932. This number is 15.9 per cent of the total 398 animals. There was at least one adult male in every group. The number per group ranged from 1 to 6, the mean being 2.7 ± 1.3. Of the 489 howlers observed in 1933, 82 were adult males or 16.8 per cent of the total population. In the 28 groups, every one had at least one male and the number ranged from 1 to 5 with a mean of 2.7 ± 1.3. As shown by inspection, there is in both sets of data (table 1) a positive correlation between the number of males in a group and the total number of individuals in the group.

TABLE 2

Classification and description of howler young

CLASSIFICATION	ESTIMATED SIZE	COLOR	RELATION TO MOTHER	TENDENCY TO PLAY	ESTIMATED AGE
	grams				
Infant 1	600	Grayish-brown	Carried on ventral surfaces of mother	+	Less than 1 month
Infant 2	900	Brownish-black	Carried on dorsal surfaces, sacral and lumbar	++	About 6 months
Infant 3	1,500	Black	Carried and occasionally assisted over critical crossings (lower incisors appear at 11 months)	+++	About 12 months
Juvenile 1	2,500	Black	*Weaning period:* associated with mother but relatively independent	++++	About 18 months
Juvenile 2	4,000	Black with reddish mantle	May be seen with mother and sibling	++	About 25 months
Juvenile 3	6,000	Black with distinctly red mantle	Entirely independent	+	About 36 months

2. The clan females (f and m). Adult females were classified

into two categories: (1) Females (f) which were not carrying infants, although they may be rather closely associated with an infant 3 (see table 2) or a juvenile 1 or 2 (see table 2), and (2) females (m) which carried infants during group progression or were closely associated with an infant 2 or 3.

The number of females of both classes ranged in 1932 from 3 to 14 per clan, with a mean of 7.4 ± 3. Females constituted 42.8 per cent of the entire population. In 1933, the range was exactly the same as for the previous year and the mean was 7.4 ± 2.8. In 1933, 39.3 per cent of the total population were adult females.

The number of females not carrying infants ranged from 2 to 10 in 1932 and from 0 to 10 in 1933, and the means were 4.6 ± 2.0 and 3.4 ± 2.4 respectively. Of the total population in 1932, 27 per cent were females not carrying young and 19 per cent were similarly classed in 1933.

Females carrying or closely associated with dependent infants were found to constitute 16 per cent of the total population of the first census and about 20 per cent of the total of the second census. In 4 groups out of a total of 51 for the two years, there were no mothers and infants, and in 1 group in 1933, 9 females were closely associated with infants. The means and standard deviations for mothers of 1932 and 1933 were 2.8 ± 1.4 and 3.5 ± 2.0 respectively. Of the total number of females observed in the two censuses, 4.06 per cent carried infants less than one month of age and 8.01 per cent carried infants of category 2 (see table 1).

3. The clan young. a. Infants. An infant is characterized by its high degree of dependence on its mother for protection, locomotion, and feeding. I have classed them into three different categories on the basis of differences in size, color, position in which carried, and degree of independence in locomotion and feeding. The arbitrary criteria for classifying infants and juveniles are given in table 2.

There were 3.8, 6.7, and 7.3 per cent of the total population classified respectively as infants 1, 2, and 3 in 1932. The following year the percentages were 4.3, 8.9 and 6.5 on the basis of the same classifications. When the figures for the two years are combined it is found that 4.1 per cent were infants 1, 8.0 per cent were infants 2, 7.1 per cent were infants 3. My estimations of the ages of these infants, as shown in table 2, are based on the close observations of wild and captive specimens. One of the captive infants was studied and close checks made on the behavioral development, size, and color changes. There is a gradual change from the infant state of dependence to the relatively independent juvenile.

b. Juveniles. Three different groups of juveniles were distinguished and designated as j1, j2, and j3. Criteria for this classification are also to be found in table 2. In 1932 the following percentages were found: j1 constituted 7.3 of the total population; j2, 10.5 of the total, and j3 made up 5.0 of the total 389 animals. In 1933 the following percentages were found: j1 were 7.6 of the total; j2, 10.5; and j3, 5.9. When the data on all 51 groups of the two years are combined, it is found that of the 887 animals 7.6 per cent were juveniles 1, 10.5 per cent were juveniles 2, and 5.5 per cent were juveniles 3. My basis for estimating the ages of juveniles is inadequate, but I suggest that juveniles 1 are about 18 months of age, juveniles 2 about 25 months of age, and juveniles 3 are over 36 months of age.

An experienced field observer who has also profited by making collections of animals, knows that late juvenile males may be taken for females. Every possible check was made to avoid a systematic error of this kind. I attempted to inspect the external genitalia by the use of field glasses, but even that did not give a clear-cut basis for judgment, for just as the testes are descending a structure is formed which, as observed in the wild, closely resembles the external genitalia of adult females. In making the census, it was a predetermined plan that when there was any doubt regarding the sex of an animal which resembled an adult female, the individual was placed in the juvenile 3 category. The reliability of the censuses is indicated, in a rough way, by the consistency of the results of the counts.

E. THE VARIATION IN CONSTITUTION OF A SINGLE GROUP. Table 3 gives a sample of the changes occurring in Group 1 for a seventeen-month period. The number of males varied from three to five. There was a decrease of two females from May, 1932, to January, 1933, and an increase from ten females to twelve during the first five months of 1933. The expected fluctuation among the young animals occurred. Between January and May, 1933, two animals are known to have been born and two young to have disappeared. Others may have been born and met with accidents. From January 1, 1932 to May 7, 1933 this group increased from twenty-six to thirty animals or an addition of only four animals which remained part of the parental group. Two of these additions were adult complemental males which joined the group, whereas others may have separated from the group. The size of a group is determined by the number of infants being born, the number of animals joining the group, the number of deaths, and finally the number of animals which separate from the parental group either as individuals or as nuclei of new clans.

TABLE 3

Variation of Group 1 at four times during the two periods of study

DATE	MALES	FEMALES		INFANTS	JUVENILES	TOTAL
		(f)	(m)			
January 1, 1932	3	7	4	4	8	26
May 2, 1932	4	10	1	1	11	27
January 1, 1933	4	5	5	5	10	29
May 7, 1933	5	9	3	3	10	30

F. THE MEAN TENDENCY OF GREGARIOUSNESS IN HOWLERS. With the data at hand, it is possible to write significant formulae which express the central grouping tendency: The formula for the mean tendency of gregariousness or the characteristic and specific mean tendency to form groups, and a formula for the proportion of animals of different categories in groups of howlers. It is permissible to combine the data of 1932 and 1933, since the factors operating to cause groups to form and to be maintained are constantly changing; hence the data for the two periods may be considered as two distinct samplings of the grouping of the same population.

I shall use the data to indicate the central tendency of howling monkeys to form groups and this will serve to characterize this tendency. I propose to express this central tendency by using the means and standard deviations of the animals of the nine categories enumerated on p. 58. In addition, a symbol of unknown quantity must be written to represent the complemental males (which are of unknown number) and the form of their grouping. I suggest *X* to represent an unknown quantity, *M* to represent an adult male and I to signify the fact that they live temporarily as individuals and not in groups. The means and standard deviations of each of these categories have been figured for fifty-one groups and the formula for the composite mean grouping tendency of howlers may be written as follows: It equals

(M 2.8 ±1.2) + (f 4.8 ±2.5) + (m 2.4 ± 1.5) + (i1 .7 ±.7) + (i2 1.4 ±1.2)+
(i3 1.2 ±1.4) + (j1 1.3 ±1.0) + (j2 1.8 ±1.2) + (j3 1.0 ±1.1) + (M_I X)

The central tendency may be expressed by using the median number for each category and for the total. The composite median grouping tendency equals:

(M3) + (f4) + (m3) + (i1, 1) + (i2, 1) + i3, 1) + (j1, 1) + (j2, 2) + (j3, 1)
[group median 18] + (M_I X)

A formula which expresses the proportions of group-living animals of definite categories may also be useful in the study of comparative sociology of animals in general and of primates in particular. This formula is similar to the other, but the number of animals of the six categories is given in terms of the percentage of the total number of animals observed. The proportion of group-living animals of the different categories equals:

(M 16.4) + (f 27.3) + (m 13.5) + (i1 4.1) + (i2 8.0) + (i3 7.1)
(j1 7.6) + (j2 10.5) + (j3 5.5) + (M_IX)

G. THE SOCIONOMIC SEX RATIO. One of the facts shown by the figures which have been presented is the disparate sex ratio of the adult animals. In 49 groups of the total 51 on which the census was made (see table 1) the number of animals classified as adult females exceeded the number of adult males. In two groups the numbers of adult males and females were equal, and in no case did the number of adult males exceed the number of adult females. Of the total 398 animals observed in 1932, 16 per cent were classified as adult males and 42 per cent as adult females. In the census of the following year, 17 per cent of the 489 animals were classed as males, as compared with 39 per cent which were classed as adult females. When the total *adult* population alone is considered, the data of the first census show that 28 per cent were males and 72 per cent were females. The difference and its standard deviation are 45.4 ± 0.32. In the second census 30 per cent were classed as males and 70 per cent as females. In the ratio found there would be 249 females to each 100 males.

Azara (5) and Rengger (53) estimated that among howlers there were about 3 females to each male. Wislocki (69) has found a preponderance of females in a collection of 179 animals. Of the adults collected, the ratio given by Wislocki (69) was 70 males to 100 females. This author writes: "The great preponderance of females in spider and howling monkeys is an interesting observation which requires explanation. Either fewer males than females are produced in these species due to an uneven sex-ratio in the germinal cells or the males are subject to a higher intra-uterine or post-natal mortality than the females." Clark supplies me with the following data: Of 65 "black howlers" employed in experiments at Gorgas Memorial Laboratory, 27 were males and 38 females, or about 41 per cent males and 59 per cent females. In a total of 314 brown howlers which have been employed, 131 of these were males and 183 females. Again, approximately 41 per cent of these 314 animals are found to be males and 59 per cent females. Clark qualifies these data, however, as follows: "It is well to remember that these are nearly all infants and juveniles. An autopsy list of old animals killed in camp would show a higher incidence of females among adults." It is a striking fact, however, that of 141 adult howlers which Wislocki shot in the wild at random, about 41 per cent were males and 59 per cent females, and that the same percentage distribution is shown by the 314 animals used by Clark.

Data from several sources indicate that the tertiary sex ratio of howling monkeys is disparate, and that there is a preponderance of females. The figures presented for the howler population indicate that the ratio of adult males to adult females living in groups is more disparate than the tertiary sex ratio. Part of this latter difference may be the result of a certain, at present unknown, percentage of the adult males living temporarily separated from groups. I am convinced, however, that this would not entirely account for the difference. The important fact from the point of view of analyzing the grouped population is that within these clans there is an average of three adult males to seven adult females.

I propose to term the ratio between the number of adult males and adult females living in semi-closed groups the socionomic sex ratio.

H. Subgroupings within the clan. A large clan of howling monkeys has numerous subgroupings of two or more kinds: (1) There are the relatively persistent subgroups lasting for months or years and (2) there are temporary subgroups. The following subgroups may be classified as type 1: (a) a female and her infant and (b) a female, an infant, and a late juvenile (see plate 6, B). Subgroupings which may be classified as type 2 are: (a) play groupings of young animals, (b) defense groupings of two or more males and at times a female, (c) directive groupings of males and females during progression, (d) a retrieving subgroup of males and females, (e) a grouping (usually females) around a mother with a new-born infant, where the focus of behavior is the new-born animal, and (f) groupings of young and males formed around an oestrous female. There may be other subgroups determined by ecological factors. Individuals in a clan do not space themselves randomly, therefore, but behave with reference to other particular animals in the clan as well as to the clan as a whole. It would seem that the strength of the bond between animals is indicated by their spatial relations and the duration of the particular spacing. The motives and incentives determining subgroupings are more easily analyzed than the entire complex of determinants operating to cause the grouping of a large clan. An analysis of these relationships will be undertaken later.

I. Summary. Study of the organization of the howler population of Barro Colorado Island was facilitated by many characteristics of these monkeys. The range in the size of groups was found to be great and there is not a strong tendency among howlers to form groups of uniform size and constitution. The total population in 1932 was found to be 398 ± 50 animals living in 23 groups, and the following year 28 groups were differentiated which contained 489 ± 25 individuals. The howler population of Barro Colorado Island seems to be increasing rapidly. Nine categories of animals were differentiated and the percentage of each category of the total population was given in this section. The results are expressed in a formula which characterizes the tendency of howlers to form groups. The sex ratio of group-living adult howlers was found to be disparate, there being a much larger number of adult females than adult males living in semi-closed groups. A few individual males live in temporary separation from groups. Within a group there are numerous subgroups which apparently are the results of variations in the strength of the social bonds among the individuals of a clan.

VIII. GROUP INTEGRATION, SOCIAL RELATIONS, AND INTRA-GROUP BEHAVIOR

Animal groupings are so complex that an adequate description demands that the many processes and aspects of group life be treated separately. There are forces which hold a number of individuals in a single group, and there are other processes which tend to cause a group to disintegrate. In a stable group these opposing forces are approximately in a state of equilibrium. The resultant of the first group or "vector" of forces is a state of group cohesion. The cohesiveness of a group is the result of the complex processes of group integration and group coördination. The term group integration is used to mean those processes, including the native propensities, which strongly and positively condition an individual to a number of other animals, and hence to a clan as a whole. By group coördination is meant the many stimulus acts and responses which relate the immediate activity of each individual in such a way as to result in unified group activity. The coördination of a group is dependent upon specific tendencies to action and upon conditioned responses which have been previously established in the processes of group integration.

In this chapter I shall attempt to describe as thoroughly as possible intra-group relations from the point of view of the overt behavior involved and to relate the findings to the general processes of the group integration of howling monkeys. For this purpose the animals of a group may be divided into three categories: (1) adult females (f and m), (2) young animals (y), and (3) adult males (M). The important elemental social relationships among these categories are: (a) female with young, f-y or m-y; (b) young with young, y-y; (c) female with female, f-f; (d) male with female, m-f; (e) male with young, M-y; and (f) male with male, M-M. A detailed description of these elemental relations and the reciprocal social behavior which occurs will characterize, it is believed, the group life of howling monkeys.

A. THE FEMALE-YOUNG (f-y OR m-y) RELATIONSHIPS. Subgroupings of individuals in a clan which have an adult female as the core are the most prominent parts of the larger group (13). These subgroups may consist of a mother and infant, and juvenile. At times other individuals are temporarily associated with them. A young howler is born into a subgrouping, frequently consisting of the mother and an early juvenile. The primary relations of a new-born animal are first with the mother and the sibling and only later does positive or negative reciprocal behavior occur with other individuals of the clan.

1. Behavior of the mother and infant soon after the birth of the infant. Three howler mothers were observed which had just previously given birth to infants. The new-born howler infant is distinguishable by its wet, matted fur of a distinctive light grayish color, and a parturient mother is somewhat sluggish in behavior and almost constantly refers her activity to the wet infant or to her external genitalia. The following observations describe the early relations of adult howlers and new-born infants:

Observation 15, Feb. 3, 1932, Group 1. The mother sat in a sharply flexed posture, and the squirming, grayish-brown infant climbed up her chest to her shoulders and neck. The infant appeared to be wet, and the mother curried and licked its fur. The climbing behavior of the infant was counteracted by the mother's actions of constantly pulling it down to her abdomen. The mother again and again put her fingers to her external genitalia and then to her mouth, but even with the use of 24-power binoculars I could not detect any afterbirth. The labia appeared swollen and were slightly parted. Around the mother and infant was a circle of other females and juvenile animals, and when the mother moved, they moved. These associated animals behaved with specific reference to the infant and would attempt at times to touch it.

Observation 16, Mar. 14, 1932, Group 5. I was observing from ambush and waiting for the last animals of Group 5 to make a crossing between two trees. A peculiar series of vocalizations was heard coming from a distance of about 30 yards. The vocal pattern began as a low crackling sound and ended as a grunt tending toward a groan. The males of Group 5 responded immediately, stopped movements of the clan, and returned toward the source of the groaning vocalizations. The sounds came closer, the males clucked, and I located the approaching individual. It was a mother which carried a small, wet, yellowish-gray infant. She was cleaning the infant with her tongue and lips and this process continued for about an hour and until darkness obscured my view. Twice the mother held the infant suspended by its tail as she examined and cleaned the belly and posterior pelvic region. The mother manipulated and apparently obtained fluid from her external genitalia on six or eight occasions, and the fluid was licked from her fingers. I saw no evidence of the placenta.

Observation 17, Apr. 15, 1932, Group 12. A mother was observed carrying a small, wet, light-grayish infant. The infant threw back its head and rested it on the arm of the mother. Three times during an hour's observation, the mother grasped the tail of the infant, held the young one suspended, and cleaned the posterior pelvic area. The infant squirmed, climbed up the mother, and then was pulled back to the abdomen. A near-by female examined the infant with her nose and mouth, and a second female came and generally explored the infant. The mother seemed to avoid these approaches of other animals to her infant by turning away from them and by pulling the infant more closely to her abdomen.

Immediately following birth, the infant reacts positively to the fur of the mother; it clings to it and may thus support its own weight without use of the tail. It climbs up the ventral surface of the mother and she counteracts this behavior by pulling it downward toward her breasts and abdomen. The objective resultants of these actions are those of frustrating and diverting the climbing activity, of conditioning the infant to remain stationary on the belly of the mother, and of bringing it into contact with the nipples and food. Soon afterwards sucking is observed.

2. Relations during early stages of infancy. During the greater part of infancy, the young ones behave with constant reference to the mother. During early infancy the young one clings to its mother almost all of the time except when she is resting, and then the infant may explore the areas adjacent to her. An observer gains the impression that the young behaves very parasitically toward its mother, while she, on the other hand, behaves with the minimum of positive reactions to it. The mother begins locomotion and the young rushes to cling to her and be carried; the infant comes to nurse and the mother postures.

3. Positions in which the young are carried. Genera of primates differ in the manner in which mothers carry their young. Infant howlers are carried on the ventral surfaces of the mothers, both on the midline and sides, until the young is approximately one month old. While making daily observations on Group 1, it was possible for me to observe a new-born infant, and to follow its development. I found that when an infant was between three and four weeks old, the position in which it was carried was shifted gradually from the ventral to the dorsal surfaces of the mother. After a transition period lasting a week or ten days, during which the infant might be found now on the back and now on the belly of the mother, the young invariably rode them other in the lower lumbar and sacral region of her back with its tail coiled firmly around the base of the mother's tail.

New-born infants apparently learn to cling to the ventral surface of the mother after repeated restrictions by her of the squirming, generalized, "random" clinging activity, and following reinforced stimulation of sucking. The ventral surface is possibly the warmest place on the mother, especially when she is seated; the food stimulation is definitely localized on her chest. The hair of her belly and sides is long and best suited for the infant's grasping reflexes. Apparently the tail reflexes are not well developed at birth. All of these determine and facilitate the adaptation of the infant to the ventral surface of the mother's body specifically and to her generally.

With development the infant becomes more highly coördinated in its movements; it begins to use its tail as an organ of anchorage. It increases in weight, hence there is an increase in the difficulty of clinging to the ventral fur, and the mother may be irritated by the clinging infant and hence force it to shift positions. The infant seems to learn or become conditioned to positions on the mother where it may be carried with the greatest ease to itself and where it interferes least with her locomotion. The final resultant of all these conditions is that for most of the period of infancy, which I believe lasts at least twelve months or until the infant weights from 1500 to 2000 grams, the infant rides astride the back of the mother with its tail curled tightly around the base of her tail (see plate 13, A).

4. Maternal aid and coöperativeness. The general impression which an observer has after observing howler mothers and infants is that the young behave parasitically with reference to her. There are, however, instances of the mother's ability to aid actively in the infant's locomotion as well as instances of coöperative behavior between them. (1) The mother will at times move out of the line of progression, go to her young one and posture so that it may easily mount her and be carried; (2) mothers will recover an infant which has fallen to the ground; (3) mothers assist their young in crossing spaces between trees over which the young could not cross without aid.

a. Retrieving of fallen young. A number of young howlers have been observed during or just following a fall to lower branches, to underbrush, or to the ground. From direct observation of falling animals, I believe that they orient during the fall with their feet toward the ground. Infants which are semi-independent in locomotion, that is, when they are from six to twelve months old, seem to fall more frequently than older animals. The following are examples of observations which were made relative to the falling of infants and the retrieving of them by the mothers (the part played by males should also be noted):

Observation 18, Dec. 26, 1932, Group 1. An infant 2 fell from a tree to a low bush and began distress vocalizations. A male and female came cautiously down a vine which hung close to the infant. The female then dashed from the vine to the bush, took the infant on her back, and returned to the tree tops and the group.

Observation 19, Apr. 26, 1932, Group 12. The sound of a breaking limb was immediately followed by the distress cries of a young howler (infant 3). Concurrently, the males in the clan began to roar and rushed down to within 25 feet of the fallen young. At the same time, several females and young dashed from one part of the tree to another as though greatly excited. The disturbance subsided as the young regained a position 60 feet above the ground.

Observation 20, Jan. 23, 1933, Group 1. Just as I was leaving Group 1, I heard an object fall to the ground. The males began to display unusual behavior, and believing this indicative of a fallen young, I returned to search for it. The males directed their behavior toward the ground as if exploring the area under the tree. I found a very young infant lying on the ground, stunned, and bleeding from the nose. It soon recovered, began the typical distress cry of an infant, and attempted to climb upward on a near-by vine and bushes. The entire clan began to react most vigorously. The males dashed here and there and roared; an adult female with an associated juvenile behaved in a frantic fashion and produced wailing vocal patterns; all individuals of the clan ceased feeding and approached nearer and nearer to the ground. I prevented the infant from climbing back into the tree, although it was constantly striving to climb upwards. The female, which I took to be the mother, came to within 25 feet of the ground and pulled in dangling vines which hung toward the infant. Never did the males cease roaring. After half an hour, I took the infant and carried it away while the mother followed me for several hundred yards, wailing pitifully in response to the distress cries of the infant. This infant, "Chita," was kept in captivity and observed for three months (see plate 15, F.).

These observations give a composite picture of the reactions of associated animals, especially of the mother and the males, to a young animal which has fallen. Animals come to react not only to the actual falling or fallen young but to the breaking of a limb, for the cracking of a limb under the weight of an animal may set the males of the clan to roaring. Retrieving behavior is indicative of the strength of social bonds between the mother and infant.

b. Aid during locomotion. There is a transition stage between complete dependence of the infant on the mother during locomotion and complete independence. During this transition stage, late infants or early juveniles frequently encounter places or spaces in the arboreal pathways over which they cannot cross without aid from an adult animal. In these situations, clear-cut examples of coöperative action occur between the mother and young.

Observation 21, Dec. 25, 1931, Group 1. An adult female in making a crossing about five feet wide between two trees, suspended herself from the terminals of two opposing branches, *a* and *b*. While the female remained thus suspended for approximately one minute, a juvenile 3 crossed over her body.

Observation 22, Feb. 17, 1932, Group 7. A mother closely followed by a juvenile 3 came to a difficult crossing between two trees. She held the terminal twigs of the limb from which she was going, jumped and caught the opposing limb which was about four feet away, and then remained suspended, holding with her tail and forefeet. The young one delayed more than a minute, then crossed over its mother's body. As soon as the young had crossed, the mother pulled herself up to the second limb and continued locomotion.

Observation 23, Feb. 21, 1932, Group 1. A mother and juvenile came to a difficult crossing (see plate 13, B). The mother suspended herself from the terminal branches and remained there while the juvenile crossed over her.

Observation 24, Mar. 11, 1932, Group 12. A juvenile 3 came to a wide crossing between two trees, postured and started to jump several times but then drew back. Shortly afterwards, the mother approached, took the young one on her back and carried it over the space. The infant then dismounted and resumed independent locomotion.

Observation 25, Mar. 14, 1932, Group 5. An infant followed its mother, lagging about fifteen feet behind her. The female had made a difficult crossing from a large limb upward four feet or more to another, a crossing which the infant could not make. After several attempts by the young to make the crossing, the mother retraced her course, (possibly in response to cries of the infant) came to where it was, placed herself across the space, and remained there while the infant climbed up over her.

These observations exemplify many similar ones which I made during 1932 and 1933. Chapman (17) has also reported an example of this type of maternal behavior.

Maternal aid and coöperativeness are further evidence for the strength of the f-y bond. Aid given to the infant by the mother is possibly a form of behavior which tends to facilitate and strengthen attachment between the two animals.

5. Maternal tuition. Howler mothers control and condition their infants by facilitating their "spontaneous" activity at times, and on other occasions by restricting it. Tinklepaugh and Hartman (61) have described these two aspects of maternal tuition for the macaque. I have already described how females restrict the climbing behavior of the new-born infants, and they have been observed also to hold infants to prevent them from moving away. Young which are play-fighting are sometimes completely inhibited by a peculiar growling vocalization produced by an adult male. Through the interaction of the behavior of individuals, social reactions are learned. Examples of maternal tuition when the activity is facilitated by the mother are, however, rare, and their interpretation is uncertain.

Observation 26, Dec. 26, 1931, Group 1. A female pulled off a terminal twig filled with buds, and after eating part of them, gave the rest to a small infant 2 which was associated with her. The infant nibbled at the food.

Mothers at times seem to assist or control their infants as they make what appear to be initial attempts at independent locomotion. The following is an interesting observation in this connection:

Observation 27, Feb. 3, 1933, Group 1. An infant 1 moved between 18 and 20 inches away from its mother. Its locomotor patterns were very poorly coördinated. The mother would permit the young one to move away from her repeatedly, then she would retrieve it. At other times, she would move away from the infant for a short distance, stop and wait until the infant reached her, and then the series of actions would be repeated.

6. Protective behavior. Infants and juveniles, until they are classified as juveniles 2 or 3, may at times be seen nestling close to the ventral flexure of the mother as she sits humped sharply forward. In this position relative to the mother, they may be kept warm and protected from wind and rain. I believe all young howlers pass the night in an inter-related posture with that of the mother until they reach the age of complete weaning. The mother supplies needed protection and an important means of temperature regulation.

I have observed females retrieve their young ones when they moved near an observer or when they approached certain other animals of the group. Infants are sometimes taken and played with or carried by animals not their mothers, and in such cases the mothers have been seen to take their infants away from the associated individuals.

Females at times hold their young as if to prevent them from falling. An infant was lying on a limb before its mother, and she, reaching out with her forepaws, appeared to be holding the infant as it lay cross-wise on the limb.

7. The specificity of the f-y relationship. Group 1 has at one time contained as many as four infants of which I could not distinguish one from another. Nevertheless, each reacted specifically to a female and each female reacted specifically to an infant. The specificity of the relationship seemingly begins when the infants are only a few days old, since infants 1 react positively to their mothers, and avoid other animals of similar size and coloring. Even these young babies seem to be positively and specifically conditioned to the familiar and avoid other strange animals.

The problem arises as to why the infants react so specifically and what sensory cues subserve the discrimination of individuals. Vocalizations may function as a basis for this discrimination.

The youngest infants produce purring sounds, similar in many respects to those made by a kitten when it is contented and in contact with a person to whom it is well conditioned. I believe the same vocalizations may be produced when the baby monkey has a similar relationship with the mother. Besides the purr, there are other cries. Differences in these vocalizations, I believe, may supplement other cues and permit differentiation of the infants by females. Young and old howlers may be observed smelling associates when making an initial contact with them and then immediately afterwards either continuing the positive reaction or withdrawing.

8. Variation in the strength of the f-y bond. Another question which arises at this point is, how long will the specific reciprocal relation between the mother and infant persist and what is the curve of increase and decline? In the new-born howler, the needs of the young organism are satisfied completely in the relation with the mother. The female is the source of all incentives which satisfy the innate drives. Her behavior, such as protection, cooperation, and aid, functions to condition the reactions of the infant positively to the mother.

It is possible that measurements of the strength of the bonds between the infant and mother would show a curve which rises rapidly during the first few weeks, reaches a climax when the infant is eight to ten months old, and then begins a gradual decline. The factors which predispose a decline in the strength of the f-y bond are little known at present. The decline in the maternal drive probably is subserved by hormone control, the flow of milk may decrease, and so on. The work of Wiesner and Sheard (68) relates to this subject for the rat. In the wild, changes in the behavior of the howler female toward the young cannot be observed clearly until the period of weaning, but with the young on the other hand, the increasing independence is conspicuous.

As the infant grows, it moves with increasing freedom over the supports afforded by the forest. Clinging to the mother during locomotion becomes unnecessary. The young apparently become capable of independent temperature regulation and do not need supplementary aid from the mother. The growing infant learns to eat more and more solid foods, especially fruits. Furthermore, play as a medium of contact with other associated animals is shown in increasing amounts. The sources or loci of incentives which satisfy the infant's needs and which function to qualify social relations positively are shifted away from the mother to other objects in the infant's physical and social environment. With this increased independence of the infant and the shift in reference to primary goals there occurs a corresponding decrease of dependence on the mother and consequently a decline in the strength of the f-y bonds.

9. The weaning period. Partial weaning of the young one occurs always prior to the birth of a sibling, and possibly during the late pregnancy of the mother. At this time attempts of the young to suck stimulate the mother to behave rather "viciously" toward it. The following observations were made of mothers and juveniles during the weaning period:

Observation 28, Jan. 23, 1932, Group 2. A juvenile 2 was cuffed severely by an associated female, presumably its mother. The young was attempting to suck repeatedly and she was avoiding it, frustrating its attempts, and mildly fighting it. The mother cuffed the juvenile and displayed her teeth as though she would bite it. This interplay of activity continued for several hours.

Observation 29, May 5, 1932, Group 1. A juvenile 1 attempted to suck from its mother but was vigorously resisted. A prolonged scuffle of typical threatening behavior ensued in which the mother snarled, cuffed the juvenile, and displayed her teeth. The interplay of action continued for almost an hour as the juvenile continued its attempts to nurse and the female persistently avoided it.

I estimate on the basis of observations on a captive animal of known age that weaning occurs when the juvenile is between a year and a half and two years old. There remains after weaning (dependence on the mother for food) and after the birth of a sibling a weakened f-y bond, as is shown by continued association of the juvenile with its mother and the infant. The subgroupings f-y-y′ are the results of these relationships. After the arrival of the sibling, however, the juvenile is replaced in the elemental f-y relationship, the facilitation of positive conditioning between the mother and juvenile decreases, social bonds between the juvenile and other associates are established and strengthened, and finally the juvenile becomes independent of its mother and self-sufficient as an individual of the clan.

B. THE FEMALE-FEMALE (f-f, f-m, m-m) RELATIONS. The adult females of a relatively stable howler clan are closely associated in a communal way. Eight or ten females with and without young may be seen feeding from the same limbs of a tree. Females, mothers, and their infants frequently rest or sleep almost adjacent to each other. The females of a clan in general follow the leading males during group progression, but they also follow one another. The social relations of the adult females of a clan are mutually interactive, communal, and peaceful.

Howler females respond in a parallel way to controlling stimulation and they are indirectly related through similarity of response to common stimuli. They sometimes react defensively to a disturbing situation with their terrier-like barks, and while so doing they mutually facilitate each other. Females may flee, conceal themselves, or become very quiet in response to a disturbance and the similarity of their behavior throws them together. Since howler females, so far as I could determine, do not react to specific males, but each female of a clan may respond positively to each clan male individually or as a subgroup, their behavior is highly coördinated.

Howler females rarely coöperate with each other regardless of the closeness of their association. Several of them may group themselves around a parturient mother after birth of a baby (see observations 15 and 17). They may touch the baby with their hands and mouths and even take it from the mother, but they give no assistance to the mother. I have observed a number of crippled females which climbed with three legs and followed the clan with apparent difficulty, but I have never seen any animal assist them. Since the speed of the group's movements is in a sense controlled by its slowest members, these crippled animals are not left by themselves. When they become separated too far from the clan, particular distress vocalizations are given, and in response to these the clan halts and waits for the laggard animals to rejoin the clan.

The females of howler clans behave in a communal manner, following the same controlling males, reacting to situations in a similar, parallel manner, and sleeping or resting in close association. Instances of competition as well as true coöperation are rare.

C. THE YOUNG-YOUNG (y-y) RELATIONS. Infant howlers develop rather well coördinated locomotor patterns when they are less than one month of age. After the infant is capable of independent locomotion and begins to move away from its mother for short distances, play becomes an important form of its activity. The amount of play rises to a maximum by the time the animal is classed as a juvenile 1, and following a period of development there is a rather sharp decline in the amount of play.

1. Patterns and types of play in howlers. Young howlers, like other genera of animals, have characteristic types of play activity. A young howler may play with its hands, feet, or tail; it may play with objects such as leaves, twigs, or fruits; but the most frequent and important form of playful behavior involves two or more young animals.

The patterns of play which involve two or more individuals are forms of activity which relate to the process of conditioning or integrating an individual into the clan. Social relations with animals other than the mother first occur with play partners. Given a propensity for play, each associated young animal becomes a strong positive incentive for each other young one, and apparently through play the young individuals below the age of juveniles 1 become reciprocally conditioned to each other.

a. Wrestling patterns of play.

Observation 30, Jan. 3, 1932, Group 1. Three young animals swung suspended by their tails while they wrestled. All four feet and the mouth were used by each during the vigorous scuffle. This form of play usually begins when one young suspends itself, starts swinging, and then is joined in the suspended wrestling by other young animals.

Observation 31, Jan. 4, 1932, Group 1. A Juvenile 2 swung down by its tail and began swinging and thrashing the air with its legs. It was joined almost immediately by another juvenile and the two animals engaged in suspended wrestling. Then, within a short time, six other animals had joined in the same play activity. This is a good example of play between two animals serving to stimulate similar responses in other associated individuals.

Observation 32, Jan. 27, 1932, Group 1. Several infants 3 were wrestling while suspended by their tails. One of them began to cuff and bite its associates, which in turn attacked the aggressive little animal and forced it from the limb on which they were playing. In howlers, wrestling may occur while the young ones hang suspended by their tails or while the participants are on large branches facing each other, but the suspended wrestling is most frequently observed.

b. Chasing type of play. Chasing patterns of play occur less frequently than wrestling. I have observed as many as six young ones following each other over a definite circuit consisting of several kinds of supports. Sometimes young following each other will make a descending jump from one branch to another and then the action will be repeated again and again.

The forms of play are simple and have little variation. As animals grow older, the play becomes more vigorous and approaches play-fighting.

Observation 33, Mar. 30, 1932, Group 1. I observed two juveniles 3 playing or play-fighting for more than two hours. The activity, in the main, consisted in wrestling, both as the animals faced each other on a limb and as they swung by their tails below it. The activity at times became vicious as one of the juveniles would force the other backward down a limb. During their scuffles, it became obvious that one of the young animals was definitely superior to the other.

The patterns of play activity engaged in by young howlers seem stereotyped and simple, but this simplicity is not proportional to the amount of playing done by the young animals. In contrast to adult animals, young ones are very active. When the average sized clan is not in progression or feeding, almost invariably groups of young animals play more or less vigorously. I would estimate that young howlers spend equally as much time in playing as in feeding.

The size of play subgroups increases with the age of the young animals until they are classed as juveniles 1 and 2, presumably when they are between two and three years old, and then, coincident with the decline in the amount of play activity, fewer animals engage simultaneously in play behavior.

2. An apparent function of play. One of the most important functions of play possibly is the rôle it serves in socializing the young animal and bringing it to find a place in the existent social form of the group. Through play the growing animal establishes positive social relations with all of the immature individuals of the clan.

Young howlers apparently compete with each other during playful activity. Individuals which show much facility in the playing activity control the course of the action to a greater degree than others. Viewed objectively, play may function to establish among young animals a dominance scale, similar in kind but far less in degree than the dominance so thoroughly described by Zuckerman (73) for the baboon.

3. Apparent antagonistic behavior of juveniles toward newborn infants attached to a female. After a young animal is partially weaned from its mother, it still associates with her and possibly spends the night in an interlocking posture with her just as it does in rest periods during the day. This association is somewhat upset when a sibling is born. The juvenile is displaced to a certain extent. I have observed several instances of juveniles 1 or 2 apparently trying to pull the infant away from the mother, and at other times, and more frequently, I have seen these juveniles attempting to wedge themselves between the young infant and the mother.

4. The decline of play and the emergence of play-fighting. As young howlers grow older, play seems to become more and more vigorous so that playing activity between late juveniles may be classed at times as play-fighting. I suggest that at this time the motivation which was sufficient to provoke overt play becomes inadequate for predisposing pugnacious behavior. As the severity of play-fighting increases with consequent pain and frustration, play behavior becomes "extinguished."

D. THE MALE-FEMALE (M-f) RELATIONS. 1. Sex differences. The behavior of adult howler males differs from that of adult females in defense situations, in a situation where a young has fallen, and in the activity of leading the clan during progression. The sex differences in behavior are equally as marked as those of anatomy.

The defense situations usually noted are those of an observer approaching a clan, when a solitary male seeks to join a clan, or when two clans come near each other. In these situations, males are more aggressive than females. The behavior of males and females differs also in situations where a young one has fallen and retrieving behavior is in progress. The males and not the females are dominant in leading and controlling the group. Detailed descriptions will show the manner in which males and females engaged in sexual activity.

2. Sexual behavior. Twenty-nine instances of primary sexual behavior were observed. Adult animals are brought into intimate contact during sexual activity and the quality of the social relations among them are thrown into clearer relief during this behavior. If males compete and fight, one would expect this to occur when there is a highly receptive female closely associated with them. If there are bonds between particular males and particular females, these bonds might be detected, it would seem, during sexual behavior. In brief, much might be learned presumably about the qualitative organization of primate groups by observing them while sexual activity is in progress. The following are detailed descriptions of sexual behavior of howling monkeys in their native habitat:

Observation 34, Feb. 23, 1932, Group 1. Five instances of primary sexual activity were observed. Two receptive females and three males participated in the activity. I entered an arboreal blind 25 feet from the ground and directly under the tree in which Group 1 was stationed, at 7:30 A.M. Male no. *1* and female *a* were lying within 10 or 12 feet of each other. Female *a* approached male no. *1* at 8:30, displayed rhythmic tongue movements, and attempted to lick his hands and arms. The rhythmic tongue movements are made by the animal's opening its mouth, protruding its tongue and moving it rapidly in and out and up and down. The female assumed sexual postures, but the male did not respond. Repeatedly the female displayed rhythmic tongue movements with reference to the male. He responded negatively to all this behavior by withdrawing.

Female *a* then gave rhythmic tongue movements with reference to male no. *2* which approached her. This male responded with similar gesticulations and copulation occurred about 30 seconds later. The postures were dorso-ventral with incomplete mounting by the male, i.e., he maintained contact with his support by using his hind legs and tail (see plate 11, C.). The duration of copulation was approximately 25 seconds, and although they were not completely discrete there were 12 or 15 thrusts.

After copulation between female *a* and male no. *2*, the female moved away from him and again approached male no. *1*. She displayed rhythmic tongue movements in several series, but the male again withdrew from her. (Note: I believe that this male had been previously satiated sexually. The female exhibited a definite preference for him over male no. *2*, and this, perhaps, may be accounted for in terms of conditioning during previous sexual activity.)

Female *a* again approached male no. *2*. Rhythmic tongue movements were exchanged, the female postured, and copulation was completed. Consummatory behavior lasted 40 seconds during which there was a period of intromission of approximately 30 seconds. About 18 thrusts were given.

Seventy minutes later, copulation occurred again between female *a* and male no. *2*. In this instance, as previously, the female initiated the behavior and seemed to be the aggressor. I could not obtain data on the phases of the copulation because of obstructions to my vision.

Male no. *3* was lying 40 feet directly above my blind and in full view when he was approached by female *b* which was associated with a juvenile 3. The female evidenced sexual exploratory behavior, withdrew about four feet, and lay down with her head toward the male. Suddenly the male approached the female and copulation was completed. The posture was dorso-ventral and the mounting posture of the male was incomplete. The total period of coverage was 30 seconds and intromission lasted 20 seconds. After coition, the female went to the fork of two limbs and rolled several times on her back, behavior which frequently follows copulation.

Male no. *3* and female *b* exchanged rhythmic tongue movements one hour later and copulation followed immediately. The female made the approach. The total period of coverage was 35 seconds and the duration of the period of intromission was 18 seconds. Following copulation, the animals separated by a distance of about two feet, and the female again assumed a position on her back and rolled from side to side.

Female *b* approached male no. *3* again after one hour and fifteen minutes. She displayed rhythmic tongue movements and provocative behavior, but the male responded negatively and withdrew. Twenty minutes later, the female again made an approach, but again the male withdrew.

The appearance of the external genitalia of the receptive females could not be distinguished from the genitalia of non-receptive animals (see photographs 16, C, G and E). A receptive howler female is identifiable, so far as I can tell, only by her behavior, for there is no swelling or reddening of the sexual skin which occurs in many catarrhines.

Observation 35, Feb. 24, 1932, Group 1. I was in an arboreal blind observing a female and her juvenile 2 feeding. The female displayed rhythmic tongue movements in the direction of two males which were also feeding about 40 feet away. Both males moved rapidly toward the female, but one arrived about five feet ahead of the other. The male which arrived first copulated almost immediately with the female and for the remainder of the day the two were closely associated. The second male followed the female also, but remained at a greater distance from her. This subgrouping was unusual, for it consisted of a male, female, juvenile 2, and a male which was not sexually active with the female. The next morning I was reasonably sure that the second male was associated with the oestrous female and the juvenile.

Observation 36, May 9, 1932, Group 1. A subgrouping of a male and female was observed when I found the group at 7:30 A.M. The female was lying with her head on the side of the male. I saw that she could be identified by a protrusion of her lower lip. The two animals aroused themselves, then the female presented to the male and urinated. Rhythmic tongue movements were exchanged between the two animals. The male was mildly aggressive and at 7:55, two minutes after the animals stirred, copulation was consummated. The total period of coverage was 25 seconds and there was an intromission period of 22 seconds.

The male completely mounted the female, a copulatory posture which I had not previously observed. The male's feet were placed on either side of the female's hips and the hands were on her shoulders. His tail was coiled around the base limb. In this case, as I had noted previously, the female moved over to the forks of a limb before copulation; possibly this is an example of anticipatory behavior.

The second copulation occurred at 8:05, after an interval of ten minutes. The male displayed rhythmic tongue movements and approached the female, thus initiating copulation. The period of coverage was 42 seconds and the period of intromission was 20 seconds.

At 8:19, after an interval of fourteen minutes, copulation recurred. It was initiated this time by the female. The periods of coverage and intromission were 31 and 23 seconds respectively. The male mounted the female completely as he had previously done, and maintained contact with the limb by means of his tail. During copulation the male showed rhythmic lateral movements of his sharply flexed legs. These movements apparently correspond to thrusts when other positions are assumed.

The female was in close rapport with the male during this period of strong sexual motivation. She constantly watched him, placed herself before him repeatedly, and varied her positions with his.

The fourth instance of primary sexual activity occurred at 8:26 o'clock. It was initiated by the female. The periods of coverage and intromission were 28 and 24 seconds respectively. It was obvious that at this time the male was becoming less aggressive and the female more aggressive.

At 8:55 the fifth instance of primary sexual behavior occurred, just one hour after I had observed the first copulation. The female in this instance approached the male and assumed provocative postures repeatedly prior to the consummation of the sex act. The periods of coverage and intromission were 24 and 21 seconds respectively. Again mounting by the male was complete. Apparently the female was still strongly motivated, but the sex drive was weakening in the male.

At this point I lost track of the animals, but again found what I am sure was the same pair of animals at 10 o'clock. Ten minutes later they copulated. There was an adjustment period of 62 seconds then, after complete mounting, 24 and 20 seconds were taken for total coverage and intromission. There were 16 or 18 thrusts.

At 10:45 these animals copulated for the seventh observed time. The actual duration of the insertion was 21 seconds, the approximate period of adjustment was 8 seconds, and there were 17 thrusts.

The decline in the *readiness* of the male to engage in sexual behavior and the increased amount of provocative behavior displayed by the female became more and more marked. The male and female consorts tended to move away from the focus of the group.

The female approached a second male, after repeated negativism on the part of the first male, but when she had approached within eight feet of male no. *2*, male no. *1* intervened. Male no. *1* moved quickly between the female and male no. *2*, thus showing slight evidence of rivalry.

Observation 37, May 10, 1932, Group 1. I located Group 1 and the female which I had observed the day before. The protruding lower lip was an unmistakable mark of identification. I saw a male copulate with her almost without any preliminaries and then leave immediately. The period of intromission was 20 seconds. This was one of few examples of copulation between animals which did not remain closely associated for a period of time.

Shortly afterwards, this female became associated with another male. Copulation was attempted but not completed because of the approach of a third male. The male consort avoided the approaching male by swinging under the limb.

For four hours I followed the marked female. Several times males approached her but she avoided them. At times males would behave as if feeding until they came near the female (sham feeding) and then they would attempt copulation. Later the female evidenced rhythmic tongue movements with reference to each of the four males in the group. When a male became associated with her, she moved away from the focus of the group. Several times the female postured, but when the male advanced she withdrew. As one male left her another approached and shortly afterwards copulated with her. The total period of coverage was 24 seconds and the period of intromission was 21 seconds. This was a second clear-cut example of a receptive female acting preferentially toward one of two males.

After further study, a situation arose in which I might have lost track of the group and the individual female, so I shot her in order to get the reproductive tract for histological study.

Observation 38, May 3, 1932, Group 1. A male and female lay close together, and from their positions I predicted that they were consorts and that sexual activity would follow shortly. The female displayed rhythmic tongue movements with reference to the male; he responded similarly and primary sexual activity occurred within one minute. The total time of mounting was 31 seconds; intromission lasted 21 seconds, and there were 23 discrete thrusts. The copulatory posture of the male was that of partial mounting. During coition, the female turned her head and displayed rhythmic tongue movements with reference to the male.

Copulation occurred again twenty minutes later, following a series of exchanged tongue gestures. There was a period of adjustment of 15 seconds and a period of intromission of 24 seconds.

Rhythmic tongue movements were exchanged twelve minutes later and these were followed immediately by copulation. The periods of adjustment and intromission were 10 and 20 seconds respectively.

After sixteen minutes copulation was repeated, but it was impossible in this instance for me to ascertain the duration of the various phases.

Copulation was repeated twenty-five minutes later. The period of adjustment had a duration of 10 seconds and the period of intromission lasted 25 seconds.

Observation 39, Jan. 4, 1933, Group at Zetek 12. This group was greatly excited because of my presence, and in order to cause the animals to continue their movement I fired a pistol. This resulted in much excitement and all males of the group roared vigorously.

I saw one of the males return over the course of march through two trees to a female which was trailing behind the clan. When he reached her, copulation occurred almost immediately. Copulation does not usually occur in a situation of this kind.

Observation 40, Feb. 3, 1933. Male-female consorts were located within the group and were identified by their positions with reference to each other and the exchange of rhythmic tongue movements or lingual gestures. These gestures were followed by consummatory sexual behavior with a period of intromission of 23 seconds. After an interval of forty-five minutes, copulation occurred again and the period of intromission was 25 seconds. Again tongue movements preceded the act. When the consorts were first observed, the male displayed rhythmic tongue movements several times but the female did not respond to them. There were no other indications of aggressiveness on the part of the male except his following the female. He stayed within 20 feet of her always and came especially close to her when other males were near.

Male-female consorts frequently become separated by a distance of from 40 to 50 feet from the clan. They also seem at times to avoid being observed by moving into thick tree tops.

Observation 41, Apr. 6, 1933. A subgrouping consisting of a male, female, and infant 3 was observed. From the positions and spacing, I inferred that the female was in a state of oestrus. Within a short time she displayed provocative behavior. Lingual gestures were repeated frequently. After contact with the male, the female would hasten a few feet from him, posture for sexual activity, continue rhythmic tongue movements, and then if the male failed to respond, she would dash back to him and lick his face. The male responded lazily, they exchanged tongue movements, and immediately afterwards copulation occurred. The total period of coverage was 32 seconds; within this period I estimated the intromission period to be 25 seconds.

Observation 42, Apr. 11, 1933. Immediately upon making contact with a group at Wheeler 17, I observed a male-female grouping. The animals lay within a foot of each other. I partially concealed myself and observed them. During the following forty-five minutes, primary sexual behavior occurred three times. The average period of coverage was about 45 seconds and I estimated the duration of intromission to average approximately 25 seconds. Postural adjustments were awkwardly established. Prior to each copulation, the female displayed tongue movements repeatedly; in quick succession she would posture and reposture, and several times she licked parts of the male's sexual anatomy. Once in response to this stimulating behavior, the male clawed at her and bit her severely enough to cause her to yelp. The female then ran quickly away but shortly afterwards returned and lay down in contact with the male. Observations continued for two hours, but there was no further sexual activity.

Observation 43, Apr. 22, 1933. I observed a male-female subgrouping and predicted on the basis of the animals' behavior that the female was in a state of oestrus. With the female was a juvenile 1 which was still sucking. Copulation occurred before the vocalizations given in response to my approach had ceased. The act was initiated by the female which displayed tongue movements and posturing with reference to the male. The period of coverage was 35 seconds and the period of intromission lasted approximately 25 seconds. About 20 thrusts were given.

One and a half hours after the first copulation, the act was repeated. There were 40 and 23 seconds in the periods of coverage and intromission respectively. Piston movements began with mounting and were repeated about 25 times.

From these examples and from other detailed descriptions of copulations, which need not be given here because of their uniformity, the characteristics of howler sexual activity become fairly clear. The behavioral aspects preliminary to copulation are the rhythmic tongue movements, provocative posturing, and exploratory behavior. This behavior should be compared with descriptions given by Zuckerman (73) of the behavior preliminary to copulation in catarrhines.

Almost invariably primary sexual activity in howler monkeys is preceded by rhythmic tongue movements, and this type of gesture is usually exchanged between the two sexual consorts. When one of the animals, either the male or the female, produces this gesticulation and the partner responds similarly, prediction can be made with high reliability that copulation will follow in a short time if distractions or inhibitory stimulation does not intervene. Either the female or the male may initiate these gestures. The patterns of tongue movement were always directed with reference to the associated consort and given when the consort was observing the act.

Various interpretations may be made of this behavior. My opinion is that the lingual gestures are specific, occurring because of strong sexual motivation with reference to a potential partner for the sex act, and that this behavior becomes so conditioned as to signify sexual readiness. It also seems significant to me that these gestures are made with the tongue, an organ which is primary in the production of speech.

Howler females evidence few forms of display. They seem at times to place themselves so that their posterior is near the muzzle of the male, but this is by no means generally true. Females may, however, prior to copulation, repeatedly assume the copulatory posture of submissiveness, and at the same time give the lingual gesticulations. These postures and the associated movement patterns appear to be very forceful sexual stimuli for the male. In addition the female may at times lick the face and hands of the male. If the male is properly motivated, he responds to this provocative stimulation; if he is sexually satiated, he may react viciously toward her as Zuckerman (73) found in the baboon.

Males show some exploratory behavior toward their female consorts. This consists mainly in smelling her external genitalia, urine or vaginal fluids, but I have never observed manual exploratory behavior.

The initiation of the sex act may be made by the male or female, depending upon the relative degrees of motivation. When a male first becomes associated with an oestrous female, he usually is the aggressor. As the male becomes more and more nearly satiated, however, there is a marked increase in the amount of provocative behavior shown by the female, and she is definitely the aggressor.

a. Sexual postures and time relations of various phases of copulation. I have observed three types of copulatory postures: (1) *dorso-ventral* with the male mounting *incompletely* but maintaining contact with his support with his feet and tail, (2) *dorso-ventral* with *complete* mounting by the male, although contact with the support is maintained by the tail, and (3) *posterior-ventral.* A single observation was made of the female's assuming a sitting posture over the male as he was suspended from several branches. Type 1 is the posture which is typical of copulation in this species.

It was possible by the use of a stop watch to make determinations of the duration of two phases of the sexual act: the period of adjustment and the period of intromission. The means and standard deviations of the period of adjustment for 19 copulations were found to be 9.7 ± 5.7 seconds. For this period there is a marked variability as shown by the large standard deviation. The period of intromission for 25 instances of primary sexual activity had a mean duration of 21.8 ± 2.8 seconds. The total period of coverage, i.e., the period during which the male was on the female including the adjustment and intromission periods, for 29 instances of copulation had an average duration of 32.1 ± 5.6 seconds. The number of thrusts ranged from 8 to 28 per copulation and averaged 16.9 ± 4.8. These data are descriptive of the characteristic temporal relations of phases of primary sexual activity in howlers.

The frequency of primary sexual behavior has been taken as a measure of sexual motivation in pairs of animals (Carpenter 16 and

Stone 60). The frequency of copulation in howlers varied greatly as shown by the time intervals between copulations in the 18 instances when I was sure that no other copulations had occurred. This period ranged from 7 minutes to 45 minutes. The average time elapsing between copulations in these selected 18 instances was 24.2 ± 14.9 minutes. Apparently the time interval between copulations increased as either the male or female or both became sexually satiated. When a female comes into a state of oestrus and becomes associated with a highly motivated male, primary sexual activity occurs with great frequency. Following an initial period of a few hours, there is a rather rapid decline in the frequency curve to the point at which the first male becomes satiated and discontinues association with the female. The female then may become the consort of another highly motivated male. The frequency curve begins again at a slightly lower level than just after the formation of the first subgrouping. The frequency of copulation, however, again declines until one of the consorts is sexually satiated. In this manner two or more males may be satiated by one female during an oestrous period. I have observed five instances of different males copulating with the same oestrous female, and I am convinced that typically more than one male copulated with a female during her period of receptivity.

Howler females are more aggressive than males in sexual activity. Either the male or female may initiate copulation when two animals first become sexual consorts. Afterwards, and until the last phase of oestrus, the female seems to be always ready for copulation; she repeatedly postures and shows other secondary sexual behavior and she usually initiates coition. The frequency of copulation seems to be limited by the reluctant responses of the males. Males have not been observed to behave aggressively toward females and dominate them during the sex act. For most of the oestrous period, females behave as if more strongly motivated for sexual behavior than are the males.

The question arises as to what conditions determine the association with one particular male rather than another when a female first becomes receptive. So far as I could ascertain, the female which was receptive but unassociated with a male displayed invitational behavior with reference to the most convenient male. This usually meant the one nearest to her. If he did not respond, another one was tried. Once I observed two males respond almost simultaneously to the lingual gestures of a female (see observation 35). The one which arrived first copulated with her almost immediately and remained a close consort for many hours. The second male followed the consorts and a juvenile, but there was never observed any vigorous competition between the two males for access to the female. However, in two instances I observed what seemed to be preferential activity of a female toward one of two males. It would seem that the sexual relations of howler males and females should not be classed as polygamous or monogamous, but if a classification is to be made, the relations might be called *communal.*

From the standpoint of our central problem, that of how individuals become integrated into a group, it is important to note that during the oestrous period of a female, she may be the consort of several males of the clan. Each male may in turn become reciprocally conditioned to her through sexual stimulation. Thus, it is probable that the adult female may in time be reciprocally conditioned to all the adult males of a clan. This sexual behavior engaged in communally, possibly functions in an important way to establish and maintain the high degree of group cohesion in howler groups.

3. Periodicity of reproductive behavior in the howler female. There are no discrete periods in the annual cycle when reproductive behavior is in complete abeyance; primary sexual activity and births occur throughout the year. Howler females have periods of heightened sexual motivation during which copulation may occur very frequently.

Wislocki (69) has previously cited the facts that there is no discrete seasonal periodicity in howler reproduction and that young of all sizes may be observed during the summer months. In the last of December, 1932, when I first observed howler groups, there were young of all ages ranging from new-born to juveniles 3 in the clans. Furthermore, during each succeeding month through May, infants were born and several stages of embryos were recovered from pregnant females in May, 1932. These findings were checked the following year and the data are conclusive to the effect that howlers are born throughout the year.

This does not mean, however, that there are not variations in the incidence of oestrous behavior of females during the year, and hence variations in the number of copulations, ovulations, and births. There may well be, as Hartman (33) has shown for the macaque and as Zuckerman (74) has pointed out for several primate species, variations in the number of fertile matings and births. It is exceedingly difficult to get data on these questions in the wild, although a series of carefully planned observations supplemented by collections would yield the desired data. With the hope of obtaining data relative to variations in the number of births at different times during my periods of study, I attempted to ascertain the percentage of infants of the classification 1 which were presumably less than one month old. The data accumulated were unsatisfactory and the populations involved were inadequate. My impression is, however, that there was a higher percentage of very young infants in the groups during late December and January than in April or May (see table 3, p. 63).

Oestrus is generally understood to mean a period of special sexual receptivity in a female. The sexual motivation of howler females is greatly reinforced for periods of two or three days, as evidenced by the frequent occurrence of primary sexual behavior. The evidence for this is as follows: During nearly two months of almost continuous observations on Group 1 made in two seasons, I found that periodically there would be a female in the group which was sexually active. The males copulated frequently with her for two or three days and then a week or more might pass during which no male-female subgroupings were observed. Suddenly again a male would be seen in close association with a female and between them copulation would occur frequently. The same female could be followed for hours and sexual behavior observed between her and clan males. After repetitions of these observations, it seems that howler females have a definite oestrous period lasting for several days.

The data do not warrant a statement to the effect that no sexual activity occurs except during oestrus. Two observations were made which suggest that copulation may occur sporadically without repetition and without close association of the female and male. On the other hand, an oestrous female, I am convinced, invariably becomes a close consort of one male or even several in succession during the period of her heightened receptivity.

b. The lactation period. Females which were consorts of males have been observed associated with young which ranged in classification from infant 2 to juvenile 1. More females with infants 3 were observed in oestrus than those with any other category of young. From these facts it may be inferred: (1) that there is a lactation period in the howler female with a duration of several months and that during this time primary sexual activity does not occur; (2) that oestrus may and usually does occur before the young one is weaned; and (3) that since oestrous females with juveniles 1 have been observed (a juvenile 1 is about 18 to 24 months old) several oestrous periods may be experienced by the female before a fertile mating takes place.

4. Accessibility of a responsive male. In a howler population organized like that on Barro Colorado Island with relatively closed societies, it is conceivable that in a group where there is a great disproportion of females, an oestrous female may not at times have access to a responsive male. For example, if in the group observed in 1933 which contained ten females and one adult male, several of the females came into oestrus simultaneously or in rapid succession, the male because of complete satiation might not respond to all of them. Situations such as this hypothetical one are possibly rare, but nevertheless in relatively closed animal societies there is a possibility of oestrous females being unfertilized because of the inaccessibility of a responsive male within the clan.

5. Sexual activity and the process of group integration. For a male which is sexually unsatiated, a receptive female is a strong incentive, and for a female motivated by a state of oestrus, a male is also a forceful incentive. The male and female "vectors" of motivation function reciprocally to bring the animals together and cause them to engage in inter-related patterns of satisfying

behavior. Through these reciprocal responses the participating animals become conditioned to each other. This conditioning process with howlers is apparently not specific and exclusive between particular pairs of individuals. That is, two animals do not become specifically conditioned to each other to the exclusion of other individuals from sexual relationships. Furthermore, the sexual motivation and needs of a female in oestrus seem not to be satisfied by the sexual capacities of any one male. As a result of these conditions a female during oestrus may be reciprocally conditioned to two or three available males in the group. In howler clans there may be an order in which the males engage with the female in sexual behavior, but I could not learn whether or not this was true. Not one dominant male but several may engage in sexual activity with an oestrous female and hence become positively conditioned to her. With repetition of the reproductive cycle in the female and with uninterrupted breeding throughout the year, the process of group integration through sexual behavior is repeatedly operative, establishing and reinforcing inter-sexual social bonds.

E. THE MALE-YOUNG (M-y) RELATIONS. In general, adult male howlers behave indifferently toward young animals of all classes. Usually the clan males behave with general reference to the clan as a whole and not to particular young individuals. In the course of events in a howler clan, however, situations do arise where males and young become specifically related. The following are observations of social behavior of males and young:

Observation 44, Feb. 2, 1933, Group 2. A juvenile 2 approached a male in a direct manner and engaged him in vigorous play. The two wrestled, tumbled, and bit mildly at each other as they showed grimacing faces and displayed their teeth. Three or four more juveniles in rapid succession joined the fray. The young animals continued playing with the old male for about five minutes until he withdrew and lay watching the play continue.

Several times I have observed a juvenile and adult male swinging by their tails and wrestling. These instances of young playing with males were always initiated by the young animals.

Males tolerate the encroachment of immature animals as is shown by the following selected observations:

Observation 45, Jan. 18, 1933, Group 5. A juvenile climbed and played over the head and back of an old male. The latter sat placidly, never reacting positively toward the young one, but never interfering with it. He later moved out of the area in which the juvenile was playing.

Observation 46, Jan. 26, 1932, Group 1. A male, female, and infant 3 formed a compact subgrouping. The infant was playing actively around and over the male. The behavior of the young one was avoided by the male several times, then he moved about five feet away from the infant and lay down. No antagonistic behavior occurred.

Observation 47, Mar. 15, 1932, Group 3. A late juvenile came close to a male and placed its nose against the mouth of the male. The young one, after further exploratory behavior, withdrew from the male which remained entirely passive.

The social contacts of males and young are usually peaceful; however, there are exceptions. Young individuals may make way for an approaching male or even quickly avoid him. The male may also evidence behavior of a slightly pugnacious quality with reference to the young as described in the following observation:

Observation 48, May 2, 1932, Group 1. A male and juvenile 1 met on the same limb and audible growls were given by both animals. The male appeared to snap at the juvenile which cringingly backed away from his advances. Both animals displayed their teeth. The baring of teeth in howling monkeys is not an invariable accompaniment of pugnacious behavior, however, for the same facial pattern is shown during play activity.

Howler males may show defensive activity in regard to the young. Often when juveniles boldly approached me one or more males seemed to watch, gave warning vocalizations consisting of a series of grunts, and finally intervened between the juvenile and the observer.

Observation 49, Jan. 1, 1932, Group 1. I was partially concealed in a tree blind when a female and juvenile 1 came within 25 feet of me. Later the juvenile approached nearer the blind as it was feeding. Suddenly a male came quickly from an adjacent tree top and, grunting as he approached, came near to me. Normally a male would have remained at a greater distance.

The play of juveniles is sometimes controlled by male vocalizations. This is particularly true of play-fighting when one of the young ones gives a cry of pain. When this occurs, almost invariably, a near-by male will vocalize by a series of grunts and the quality of the juveniles' behavior changes immediately.

I have described the reciprocal behavior of males and females while retrieving a fallen young (see observations 18, 19, and 20). When a young animal falls, the males are forcefully aroused. The frequent roars, sometimes occurring as often as every twenty seconds, and the approach toward the young one are typical responses of the males to a fallen young. The following observations are significant in showing how a male may react positively and coöperatively toward an infant in an unusual situation:

Observation 50, Apr. 12, 1932, Group 6. I proposed to collect the female of a male-female-infant subgrouping in order (1) to secure an oestrous female specimen and (2) to learn the reaction of the associated male or males toward the dependent infant left without a mother.

At 7 o'clock I located Group 6 and found within it a subgroup of the desired constitution. One hour later, sexual activity occurred and soon afterward the female was shot. The young one fell with the mother to within 25 feet of the ground, but at that level it clung to branches and began to climb back into tall trees. The male consort, although he had passed into adjacent trees, returned and retrieved the infant 3. He took it on his back; the infant rode in exactly the same way that it had on its mother, and was carried to adjacent trees 60 feet from the ground.

Observation 51, Apr. 13, 1932, Group 6. I located the group again and observed it for several hours. An infant 3 was with one of the males. Wherever the male moved, the infant followed. The young animal was not assisted by the male, but finally the infant was allowed to mount his back.

Observation 52, Apr. 15, 1932, Group 6. Again group 6 was located and the behavior of the male and infant 3 observed. The infant was following the male very closely but not being carried by him. Once the infant nestled in the lap of the male as he sat on a limb; it moved out to eat some buds and then returned to him. He seemed to slow his pace several times and wait for the infant to approach him.

The number of direct reciprocal behavior patterns between males and young is very small compared with the times when inter-related behavior is possible and yet does not occur. Nevertheless, young howlers are constantly orienting themselves with reference to the adult males, the leaders of the clan. Especially during progression, they follow the males and respond to cues from them.

The M-y relations are such in howler clans as to strengthen and facilitate the process of integrating the immature individuals into the group. Were adult males antagonistic toward young, the typical high degree of cohesiveness in howler clans would not be found. The evidence does not show that howler males are antagonistic toward growing animals, but it is possible that some conflicts may occur with the very late juveniles. In general, I believe, the M-y relationships and reciprocal behavior supplement the integrative processes of maternal relations and play relations, and hence social bonds of the young animals with the group are strengthened.

F. RELATIONSHIPS AMONG MALES (M-M). There are three kinds of relationships among howler males which may be described separately: (1) Relations among the integrated males of a group; (2) relations between the clan males and the individual complemental males, and (3) relations between integrated males of two or more clans which happen to be in close proximity. This last topic will be discussed under the heading of inter-group relations.

1. Relations among adult clan males. I have already described the relations among males when there is an oestrous female present, and I have pointed out the coöperative responses of males in defense situations and when a young animal has fallen.

The males of a clan evidence the highest degree of integrated behavior during the barking, roaring type of vocalization. As a rule, every male of the clan participates simultaneously in the roars. In some situations, each of the males of the group appears to be equally and simultaneously stimulated. For example, when an aeroplane passes overhead, when an observer approaches in full view, or when two clans are arrayed for a battle of voices, all clan males roar together. The males as a group may respond to the barking of a female or to the cry of an infant. Any situation which stimulates defensive vocalizations brings about coördinated and facilitated behavior from the males of the clan.

Howler males behave in a communal manner when leading a clan. In conditions where there is a network of arboreal pathways or a lack of clearly defined routes, much exploratory "random" seeking behavior is shown. Each male of the clan participates as a rule in this exploratory behavior. In novel situations, one animal does not set off in a given direction with the rest of the clan and the other males following sheep fashion. Prior to progression, every male may actively explore, move here and there, follow a route for a short distance, and then return to the clan. When a male finds a suitable route, he will give the deep clucking vocalizations; then the females and young begin to follow him slowly, and associated males cease their exploratory behavior and fall in line with the moving column of animals.

I have not observed any instances of fighting or contention between the adult males which are well integrated into a clan. The relations among clan males are best described, so far as my observations show, as being peaceful and coöperative. Howler males have not been observed to compete for sexually receptive females, for food, or for positions.

The fact that pugnacious behavior rarely if ever occurs, possibly affects indirectly the processes of group integration and the degree of group cohesion found to exist in howler clans. The characteristic relations among males and the lack of a sharp gradient of dominance and submission are necessary to the communal type of grouping found.

2. Complemental males and their relations to clan males. Complemental males are infrequently observed on Barro Colorado

Island. I saw only five of these animals in 1932 and six in 1933. The following observations are selected from those made on solitary animals:

Observation 53, Jan. 6, 1932, near Pearson 1. This solitary male was observed for several hours. He was normally active in climbing and jumping as well as in feeding. I judged the animal to be a late adult. He had a wounded left eye and his scrotum was very large, pendant, and whitish.

I climbed the tree in which he was located and came within 25 feet of him. At another time a second observer approached this animal equally as closely. The animal did not withdraw or roar as do males of a clan when approached by an observer. This solitary male was observed on several consecutive days in the territory around the Laboratory.

Observation 54, Jan. 5, 1933, Snyder-Molino O. I observed a solitary male feeding and sought to photograph him. He was a splendid specimen with a glossy coat and clean perfect teeth which could be observed when he yawned. His locomotion was normal and he fed actively on figs and leaves. When I approached he did not howl, but lay down on a limb and watched me closely. Several times he yawned. After staying near Snyder-Molino for two hours, he moved toward Group 1 which was approaching Barbour 6.

Observation 55, Apr. 14, 1933, right of Drayton 6½ N.W. I followed in the direction of grunting vocalizations and found a solitary male feeding on figs. The individual was very active, handsomely colored, and appeared in excellent condition. He did not seem as large as the average adult male howler, and his scrotum was rather small and not as pendant as those of some other males. He seemed very wild and attempted to escape when I approached him. He did not vocalize on seeing me but seemed to attempt concealment after I had prevented his escape. Later he approached a large group of animals which were feeding several hundred yards away, and I believe that he later joined this group.

Observation 56, Apr. 22, 1933, near Zetek 6. I was observing a large group of animals from ambush when suddenly the clan males began to roar. I saw a single male cross into a tree in which there were several mothers and young. Four males of the clan hurried toward the single male and continued their intermittent, roaring bellows. The complemental male hastily retreated into the tree from which he had come.

Observation 57, Feb. 7, 1933, Group 1. A solitary male which was approaching Group 1 was carefully watched by one of the males of the clan. The clan male displayed a typical example of rage behavior in howlers. He dashed from one part of a tree to another; he bowed his back sharply and grunted, following this with a long, loud bellow; he grasped nearby branches and shook them vigorously. Always his position was one between the complemental male and the clan.

Observation 58, Feb. 8, 1932, Group 1. The males of Group 1 began vigorous and frequent vocalizations at 7:15 A.M. Their behavior was directed from Donato 1 to Lutz 1 and after a careful search I located a solitary male on the other side of the ravine about 50 yards away. This male and most of the group were in perfect view, and with 24-power binoculars I was afforded an almost perfect situation in which to observe the reactions of a clan to an approaching male without myself being a part of the affective social situation.

The roars of the clan males continued with an average frequency of one roar per minute. Occasionally the solitary male barked feebly. He became greatly excited, rushed from one branch to another and looked toward the group across the ravine. The group males displayed typical rage behavior as they shook themselves, shook branches and continued to roar, each individual male joining with the rest.

After several hours, the complemental male began to behave as if hiding himself in a tree top behind a tree trunk and in dense leaves. Finally, the lone animal shifted his position frequently and began to withdraw, and eventually disappeared from sight. The vocal battle had continued for four hours, and I estimate that about 240 group roars were produced in that time, each of which could have been heard for two miles across the lake.

Observation 59, Feb. 21, 1932, Group 1. I was in an arboreal blind at Barbour 2 observing Group 1 when the males began howling rapidly and ferociously. For two hours and a half the intermittent roars continued, at times being produced by most of the adult individuals in the clan but primarily by the males. From my location I could not discover a provocative cause and I left my blind to search more carefully. Fifty yards away toward Shannon 1, I found a complemental male. This animal was a fine specimen and approached within 25 feet of me, behaved somewhat aggressively, and then yawned. With continued roars coming from the clan, the complemental male withdrew in the direction of Shannon Trail.

The individual males which I have observed were not completely isolated from groups. They were not "solitary." From groups they came, and back into groups they eventually returned. This fact is shown not only by the attempts of these males to join groups, but by the fluctuations of the male population within groups. During my first period on Barro Colorado Island, the male population of Group 1 varied from three to five adults, and during observations in 1933 the variation was exactly the same. The group would have during one day, a change in the number of males, either one more or one less. At times the complemental males join groups rather suddenly, but relations with clans are not always established or broken suddenly. When I returned to Barro Colorado Island in December, 1932, I found an almost ideal set-up for studying the gradual adaptation of a complemental male to Group 1. Some of my notes follow:

Observation 60, Jan. 5, 1933, Group 1. The solitary male which I saw attempting to join Group 1 and which was so distinctive in coloration (M.r., see p. 52) was observed for several hours. He was a good physical specimen. His locomotion was perfect; his teeth were long, clean, and white; he had no scars or bot-fly larvae; laterally, his hair was very reddish-brown and longer than is usual. I judged him to be an early adult.

The movements of this male were always made with reference to the clan. Time and again he approached within 30 yards of some of the animals of the clan, but each time one or two males would either intervene between him and the group or they would follow the complemental male as he withdrew.

Observation 61, Jan. 18, 1933, Group 1. I was observing Group 1. The males of the clan, four in number, began the barking roaring vocalizations, grouped themselves and moved away from the focus and border of the clan. I hurriedly followed them, and found that the males were directing their behavior toward the complemental male. Voluminous roars were given by the combined efforts of the four clan males and M.r. withdrew closely followed by the clan males. They followed him about 50 yards, and then retraced their course and rejoined the clan. I saw M.r. several times during the remainder of the afternoon, randomly feeding.

Observation 62, Feb. 10, 1933, Group 1. I observed M.r. as he again moved tangentially to Group 1. He approached near the clan, whereupon the clan males bunched together and moved toward him. A series of several roars followed. There were two conspicuous gashes on the left hip of M.r. One gash was about three inches long and extended up and down his leg; the other was across the leg above the knee and at the base of the long cut. The wounds could have been made by the bite of an adult howler; the long gash by a canine tooth, the lower wound by the incisors.

Observation 63, Apr. 6, 1933, Group 1. M.r. was still following Group 1 after four months, during which time gradual adaptation to the group and the group to him seemed to have occurred. The males of the clan were still antagonistic to him as shown by their vocalizations and the direction of their behavior. However, M.r. was much more closely associated with the clan than he was last January. Twice I saw him approach females of the clan and evidence behavior anticipatory to sexual activity. He apparently is becoming gradually integrated into Group 1.

Thus it is seen that complemental males may become adapted to a group suddenly, or gradual adaptation may occur. I believe that complemental males which become associated with a clan suddenly have been a part of that clan previously, whereas when the male is from another group, the adaptation process is more gradual. This seems to be especially true when the complemental male is conspicuously different in appearance from the clan males.

Male howlers living in temporary disassociation from groups are truly complemental to the males of the clans. Through them, cross-breeding among the semi-closed groups occurs.

Complemental howler males are of various ages. One I judged to be very old; another which suddenly joined Group 1 in May, 1932, had his canine teeth broken and large sores on his hands; the solitary male, M.r., and the one observed near Drayton 6½, I judged to be young adults; on Coiba Island I collected a young complemental male howler whose testes were just descending into the scrotum. Collected specimens and observations on three subspecies convince me that complemental males have an age range from early adulthood to senility.

These males are not all unhealthy, decrepit animals driven from the group by the "fittest" or the most healthy animals. Infirmities are not the only causes of the segregation of males, for complemental males are frequently young active animals. They are not animals which are no longer capable of keeping pace with the group. Were this true, females as well as males might be found living separated from the clans.

These observations indicate typical reactions between the males of groups of howlers and complemental males which live temporarily separated from groups. The reactions of the clan males are antagonistic, whereas in most cases which I have observed, the complemental males react positively to the group. I observed no actual cases of pugnacity between clan males and complemental males, but loud barking roars functioned to drive the single males from the group. At times a complemental male may suddenly become a part of the clan, but at other times the foreign male becomes gradually conditioned into the group.

G. SUMMARY. In this section, intra-group behavior and social relations have been described and related to the processes of group integration. The new-born animal becomes strongly conditioned to its mother through the characteristic relations with her. The primary needs of the infant are satisfied by the mother, and this satisfaction facilitates and strengthens the social bond between the two organisms. The social relation between them is specific. The process of weaning alters the pre-existing m-y relation.

With increasing independence and self-sufficiency, the young animal forms, chiefly through play behavior, positive bonds with other young animals of the clan. The amount of play shown by young howlers varies during their development, increasing until the animals are classed as juveniles 1 and then declining rather sharply. I have postulated in this section that play-fighting tends to extinguish true play.

Positive attractions between the sexes advance further the processes of group integration. The apparently communal mating might function to condition each adult male reciprocally with each adult female of the clan. This process of group integration, through sexual stimulation and response, is operative during oestrous periods of the female throughout the annual cycle.

Adult males within the clan behave in a peaceful, coöperative manner, and this is an important condition for the type of communal grouping found in howling monkeys.

Clan males react antagonistically toward complemental males. The latter are sometimes driven away from clans by vigorous vocalizations of the group males. Complemental males are only temporarily separated from groups and apparently they function as cross-breeders between the semi-closed howler groups.

IX. GROUP COÖRDINATION AND CONTROL

It is difficult to analyze by observational procedures the behavior which subserves group coördination and control. It is desirable to record objectively and quantitatively the coördinating stimuli produced by one animal and the immediate responses of other animals to these stimuli, but until this is possible, qualitative descriptions must suffice. The stimulating patterns of *movement* and *sound* shown by some animals with the resultant responses of associates can be observed and recorded.

A. THE PROCESS OF RECIPROCAL STIMULATION AND ITS DEVELOPMENT. Specific movements and vocalizations occur in howler groups when the animals are immersed in an environmental matrix, and the behavior corresponds to the stimulus flux. However, animals of different categories respond differently. After the primary response has been made by one or a few individuals, their responses become parts of the situation to which other animals of the clan react. After many repetitions of a particular situation followed by specific movements, gestures, or vocalizations these become condensed and meaningful cues for associated animals and signify a particular kind of situation. It is unnecessary to assume that the animal or animals producing the primary responses "intends" to "communicate" with associates. It is unnecessary to infer that the animal making the primary response has "foresight" of the impending responses of associated animals, although an individual may *learn* that a particular vocalization, at first given spontaneously, is a means of provoking a particular response in some associate. Later then a specific response may be made as a means of provoking a certain response in other animals. In this section particular gestures, vocalizations, and other behavior patterns will be described as well as the reactions of associated animals to these stimulus acts.

B. Contact control. The coördination of behavior of howlers in its most elemental form probably is that which occurs between two individuals, e.g., a female and a very young infant. The mother manipulates the young infant; she pulls it down to her mammary glands; adjusts it to her abdomen; and prevents it at times from moving away from her. She may force it to assume a definite position during her locomotion. After repeated control of the infant by forceful handling, certain mere preparatory movements of the mother come to signalize or signify to the infant the action to follow. It becomes no longer necessary for the mother to place the infant on her belly when she is about to begin locomotion, but movements preparatory to locomotion function as signs in response to which the infant mounts its mother and postures on her for being carried. Thus in the very early infant, forced or contact control is gradually eliminated, and instead, infants respond to condensed movement cues of the mother.

C. Distant signalization. As the infant develops, there occurs an extension of the coördinative processes by distant signalization. For example, when an associated young animal swings from a limb by its tail, gives a characteristic little chirping grunt, at once several other young animals rush to engage it in play. An immature animal may begin running and jumping; others show similar behavior; and through vocal and movement cues their activities are synchronized or coördinated. A juvenile may bare its teeth, rush toward a partner and bite it, and after many repetitions, the second individual responds by withdrawing or attacking after the initial display of teeth or even after a quick forward movement.

The behavior of posturing also functions significantly in coördinating the actions of howlers. It seems as if certain postures become meaningful patterns of stimulation to associated animals, and postures, depending on their kind, may divert or facilitate action. Frequently I have seen an animal suddenly crouch at the sight of me, and other animals which could not have seen the source of the original disturbance, but which did "attend" to the crouched animal, immediately stopped moving and also crouched. Progression would cease until the controlling animal resumed locomotion. Sexual motivation in the male is most strongly reinforced by repeated posturing of the female before copulation. The presenting of female howlers arouses the sexual response in a highly motivated male. If, however, the male is not sufficiently motivated for an immediate response, the female repeats the acts, thus reinforcing the stimulation until a threshold of excitation is reached and the male responds fittingly. Posturing and gross movements function as a signal to associated animals and as coördinating stimuli for their social behavior.

D. Gesticulation. Limited and stereotyped patterns of action or condensed cues given by an animal may stimulate specific responses in associates. The most striking example of this kind of signalization is the rhythmic tongue movements which occur in howlers prior to copulation. Apparently a high state of sexual motivation plus the presence of a potential sexual partner set off in an animal the lingual gestures which have been previously described. If the animal of the opposite sex toward which these gestures are directed is sufficiently motivated, it responds with similar gestures. The exchange of these patterns made by the tongue, a social response which establishes a high degree of coördination between two animals, is anticipatory to actual copulation. The gestures seem to become conditioned stimuli signalizing a potential readiness for sexual activity.

E. Vocalization. Howler monkeys respond specifically to vocalizations of associates. I shall describe several of many vocal patterns to which specific reactions occur (see table 4).

Voca ctions

TYPE	STIMULATING SITUATION	SUBJECTS	VOCAL	RESPONDING	RESPONSE	FUNCTION OF VOCALIZATIONS
1	Disturbance: Enemy, complemental male, observer, wind, rain, aeroplane, another clan, a fallen young, etc.	Usually clan males and occasionally a clan female.	Males: A vol roar, low-pi rous. Femal bark.	the clan and ard which be- directed.	Animals of the clan show anticipation of aggressive or defensive action; may become quiet, conceal themselves. Objects of action may respond similarly or withdraw from the group.	A means of defense substituting for contact pugnacity. Regulates inter-group relations and unifies and directs clan action.
2	Precurrent to group progression and during movement of the clan.	The leading male.	A deep metalli -irregular int	ls of the clan.	Start of progression, orienting toward and moving with leading animal.	Initiates progression, controls its direction and rate and coördinates the animals of the clan.
3	A mildly disturbing and "apprehensive" situation.	An adult male.	A series of g crackling so inhaling th vocal mecha	males.	Similar vocalizations and activity precurrent to defensive action.	Prepares males for and coördinates males in defensive activities.
4	When a young has fallen.	Mother of the fallen young.	A wail ending groan.	t and other ani- e clan, especially	Young moves toward mother, males vocalize Type 1 and and move toward the young.	Aids in the finding and retrieving of the fallen young and coördinates group behavior to this particular end.
5	When a young has fallen.	The fallen young one.	A series of c sisting of th	others of the ially the males.	Movement toward and searching for the fallen young.	Location and retrieving of the fallen young.
6	Contact with a mother.	An infant or early juvenile.	A purr of seve tion.		Positive response with coddling.	Facilitation of the mother-young relation.
7	Situation provocative of play.	Playing young animals.	A little chirpi	re associated in	Playing and at times a re-orientation of play.	Facilitation and coördination of play activity.
8	Situation in which young are play-fighting with cries of a young animal.	A near-by adult male.	A grunting so	ch are play-	Cessation of play-fighting and either continuation of play or quiet.	Coördination or control of activity of young by an adult male.
9	A situation with strange or novel elements.	A male or males.	A rapid grunti who! who!	ls of the clan.	Becoming quiet or giving attention to vocalizing animal.	Directs behavior of the clan.

The most easily observed and clear-cut example is the vocalization of a leading male at the beginning of and during progression. The vocal pattern consists of a deep, hoarse cluck which may be given in series or singly. Under certain conditions it is repeated at frequent intervals. A leading male produces the sound which initiates progression and is the directive cue for other animals during progression. The sound is almost invariably given just prior to the movement of a clan from a lodge or food tree, and is repeated at intervals while the clan is moving. I found it possible to predict, after hearing this cluck, that, conditions remaining constant, the clan would very soon begin progression. The probable direction in which the clan would move could be estimated from the position of the male giving the vocal signal and the reference of his behavior. The animals of the clan respond specifically to the vocal clucking by preparing to follow the animal giving the signal. If he begins to move, the rest of the clan follows him, and it seems that by his movements and vocalizations he controls the initiation, direction, and rate of progression. The clucking vocalizations have not been heard except at the beginning of or during progression. Also the sounds are produced, in the main, by one animal at a time, i.e., the one controlling the movement of the clan. After observing hundreds of instances of the sequence of vocalization and behavior, I have become convinced that the deep cluck is given as a signal which initiates and directs, as its absence inhibits, group progression.

There is another type of vocalization which is a specific means of signaling among the males of the clan. The vocalization is produced only by males and responded to by adult male associates. The vocal pattern is a deep gurgling sound given in a series. The vocalizations might be described as a series of rapid grunts, sounding somewhat like water being shaken in a jug. The situation in which this vocalization occurs is one of apprehension, that is, just at the beginning of a series of events which may result in defensive vocalizations. A clan might be at rest, and as an observer approaches nearer, one of the males orients toward him, becomes more and more excited, and then gives the gurgling grunts. Until this time, the other males may not have been aroused, but now they respond toward the source of disturbance, and behave as if anticipating defensive behavior and vocalizations. The grunting vocalizations are not reacted to by the females and young of the clan. I believe the function of this particular vocalization to be that of coördinating the behavior of clan males specifically.

A third type of vocalization illustrative of coördinative vocal behavior is given by a howler mother when her young has fallen or has been otherwise removed from her. The pattern consists of of a wail made on inspiration of air, followed by a groan occurring with expiration. The sound can be poorly imitated by restricting the larynx, forcibly taking a deep breath, and suddenly releasing the pressure with a groan. These distressing sounds may be repeated by a female at intervals of a minute or two and continue for hours or until the young one has been recovered.

In the same social situation which stimulates the wailing groans in the mother, there occurs a specific vocal pattern in the infant. The sounds occur usually as a series of three notes or little cries, with the first fairly high pitched, the middle note higher, and the the final cry lower than the first. The series, which lasts for two or three seconds, may be repeated three or four times each minute until the infant is recovered or exhausted.

The wailing groans of the mother function in two ways: to produce stimulation to which the infant may orient and move, and to focus the activity of the clan, especially the males, on the recovery of an infant. The cries of the infant are cues which localize it for the animals which might retrieve it. The two series of vocalizations coördinate the behavior of several individuals while retrieving the infant.

Inhibitory or diverting effects. The vocalizations which I have just described have positive facilitating effects. There are other patterns which "inhibit" or divert activity. The roaring bark, which I have frequently mentioned, diverts the activity of feeding, of progression, and even of play among the individuals in the clan. The composite behavior of the clan may be characterized as anticipatory to defensive actions. During play-fighting, juveniles sometimes become rather rough and bite each other, causing yelps to be given. Near-by males respond to this situation with a kind of growl, and following the growl, I have frequently seen the juveniles immediately cease playing. The timing of the responses leaves little doubt that the young are responding to the vocalizations of the male.

Vocal signaling coördinates the activity of a group in the following ways: (1) A central source of stimulation causes numerous animals to respond in a similar way. (2) A vocalization such as a warning signal or roaring barks predisposes a behavioral attitude which is current throughout the group. (3) Particular patterns of sound effect specific responses in one kind or category of animal, e.g., the clan males. (4) An exchange of vocalizations between two animals may function to synchronize their behavior.

I have described nine types of vocalization in table 4. The vocal responses of certain animals to definite situations, the response of associated animals, and the probable function of the stimulating vocal patterns are summarized in that table. It is believed that extension of this kind of study of vocalization, and more complete descriptions of the stimulation, vocal pattern, and social responses of associated animals, will lead to a more comprehensive understanding of the coördinative processes of group action.

There are numerous other types of vocalization given and used by howlers which I have not described. There are probably fifteen or twenty distinct and important vocal patterns in their repertoire, but it is impossible for me to describe all of them in a satisfactory way.

I have learned from the study of vocalizations that the patterns vary greatly in degree of specificity in the situations giving rise to them, and specificity of the responses stimulated in other animals. Type 1 vocalization is elicited by numerous kinds of disturbing situations, and the resulting responses of associates are rather generalized. On the other hand, type 2 vocalization occurs in a rather specific situation, with the animals predisposed to progression and the very definite reactions of beginning progression and following the male.

F. Summary. Certain aspects of the complex process of group coördination have been presented in this section. Seemingly gross movement, more specific and limited gestures, and numerous vocal patterns are coördinative stimuli. I have suggested that unconditioned behavior patterns and vocalizations which are characteristic of the species and which occur in more or less specific situations come to function as stimuli or condensed cues for evoking reactions in associates. I have postulated a hierarchy of social coördinative processes which includes (1) contact control and (2) distant signalization, involving (a) gross movements, (b) gesticulation, and (c) vocalizations. Examples were given of simple coördinating processes in which gestures and vocal patterns function as determinants of final responses in other animals.

X. INTER-GROUP RELATIONS AND COMPARISONS OF SPECIES AND SUBSPECIES

A. The formation of new clans. Besides the forces operating to integrate individuals into a clan, conditions arise which cause clans to divide. Subgroups may split off from parental groups. Thus new clans are formed. These new clans are then maintained as relatively discrete, semi-closed societies.

The observations which I have made suggest that the nuclei of new groups may have their beginnings in at least three different ways: Groups may divide, strongly integrated subgroups may separate from the main body of animals, and some individuals of a clan may become associated with a complemental male. Large groups sometimes separate into two parts, as the following observations show:

Observation 64, Feb. 8, 1933, Group 1. At 8 o'clock one evening after it was quite dark, the animals of Group 1 began to vocalize. The group roars were very frequent and indicated to me that the clan had been greatly disturbed. When I located the clan it had begun to move, although the night was very dark. (This is the only instance of progression during the night that I observed.) At that time, the group was divided, one part being separated from the other part by about 50 yards. For almost an hour the males continued to roar and then settled down for the night. I could not discover what had disturbed them.

I found only about sixteen animals at 6:30 the next morning in the place where I had left the clan the previous evening. After observing these for about an hour, I heard some howlers about 200 yards away and immediately ran to locate them. I found them moving rapidly toward those which I had been observing. Ten minutes later, the two bunches of animals united without the usual vocalizations which occur when two clans come close together.

I believe that some predatory animal disturbed the group, caused it to divide, and that next day the animals re-united. A group which was differently constituted might have remained separated and thus a new clan would have been formed.

The division of a group may come about because of the fact that the leaders of the clan are either not coöperative or because they become antagonistic to each other. Males which are equally effective in leadership may, by leading parts of the clan in different directions, cause a group to divide into two parts. Presumably those animals most strongly conditioned to a particular male would follow him.

Very large groups seem to split up because of the impossibility of the proper coördination of all animals in a single body. As the clans increase in size, it appears that the difficulty of coördinating its movements by vocalization or gesticulations becomes geometrically more difficult. Also with an increase in the number of males, there is an increase in the number of potential independent leaders of a new group.

Subgroups with marked cohesiveness have frequently been observed at a distance from the main clan. I have sometimes seen a male-female-young subgrouping fifty or seventy-five yards from the main clan. Such a subgrouping may become the nucleus of a new clan. In fact, the constitution of small, and I believe new, clans corresponds closely in some instances to subgroupings. Males associated with females during their oestrous periods seem least coördinated in the group and hence are most likely to diverge from it.

It is conceivable that in a large group of animals there are subgroups whose individuals are very strongly and reciprocally conditioned, whereas these animals are only held to other members of the clan by diffuse or indirect bonds. A subgroup thus mutually conditioned would be in a state of readiness for splitting away from the indigenous clan by a process of group mitosis.

Every group, however small, has been observed with at least one male. This indicates either that the male was with the female and young when they separated from the clan or else that a male joined the female and young between the time of separation and the time when they were observed. If females and young ever become separated from their clan, a phenomenon which I have never observed, complemental males might very probably join them. It seems most probable, however, that each part of a group which separates has with it at least one male.

Another possible way in which new groups are formed, and one for which I have some data, is for several clan animals to leave the group and become associated with a complemental male. Twice I have seen females become temporary consorts of males which moved on the margin of clans and which were poorly integrated into the group.

B. The relations among clans. One of the most impressive periods of the day in the forest of Barro Colorado Island is that of dawn, and one of the most conspicuous aspects of this period is the roaring howls of the howling monkeys. Invariably, as light comes some clan or clans will break forth into howls, and these will be followed by similar roars from groups in adjacent areas. The vocalizations then spread from clan to clan until the majority of the groups on the island have howled. Again about the time when groups first begin progression during the early morning, rather general howling occurs. These vocalizations function, apparently, as stimuli of inter-group stimulation at a distance and signalize the location of the various groups. I believe the roars are important in partially determining the direction of group progression and in regulating the territorial ranges.

An observer of howlers becomes curious about the behavioral interactions which occur when two clans come together or closely approximate each other. One wishes that he might experimentally arrange such a set-up. Persistence and vigilance may compensate for lack of ability to control situations, and groups may be observed eventually in contact and in close proximity to each other. The following records are results of observations on clans reacting to each other:

Observation 65, Mar. 4, 1932, Groups 3 and 6. For several hours I had been observing Group 3 feeding from a fig tree to the right of Wheeler 18. There were sounds of approaching animals coming from the left of the trail and in the direction of the fig tree. Group 6 began progression in the opposite direction and toward Drayton Trail. When this clan had withdrawn, after a few exchanges of roars, Group 3 moved into the fig tree and fed. No antagonistic behavior other than the vocalizations occurred.

Observation 66, Mar. 8, 1932, Groups 4 and 6. "Mexico" and I came upon a large number of animals at Wheeler 24. They were greatly excited and there were repeated roars and some rage behavior on the part of several males, but no actual conflicts occurred. A complemental capuchin male was with the group temporarily. During the excitement, sexual activity occurred between two consorts. While I attempted to count the animals, the group divided, some going south and the others east. I counted those moving east and identified them as Group 6. After six hours of observation of this group, the other animals approached and were identified as Group 4. As Group 4 approached Group 6, males of the latter group met it and the direction of movement of Group 4 was reversed, after a series of vigorous and frequent vocalizations had been exchanged.

Observation 67, Apr. 26, 1932, Groups 13 and 14. Groups 13 and 14 (later identified) divided and began progression, after two hours of vigorous vocalizations toward the observer. Just prior to my reaching these animals, a series of howls was heard and I inferred that the roars were provoked by the two groups coming together. When I became the focus of action for both clans, inter-group vocalizations temporarily ceased.

Observation 68, Jan. 20, 1933, Groups 1 and 2. I located Group 1 at 8 o'clock and found a situation very favorable for observing behavior toward another group as well as toward a complemental male (M.r.). I made observations from a steep hill and into and across a deep ravine. Group 1 was 25 yards away directly across the ravine, M.r. was near me, and animals later identified as Group 2 were located 50 yards up the ravine to my right. Group 1 began progression toward Group 2, but after an exchange of vocalizations, reversed its direction. The males of both clans were greatly excited, dashed here and there and roared. The excitement was apparently exaggerated because of the presence of the complemental male.

M.r. reacted positively to Group 1 but was driven back by the antagonistic vocal behavior of the clan's males. He then behaved as if hiding himself.

Group 1 made off toward Shannon 8 and was followed by Group 2 for 50 yards. Group 2 then moved rapidly and intervened between Group 1 and the territory to the right of Shannon Trail. The two clans came to rest about 40 yards apart, and intermittently the vocal battle was renewed. On the following day, Group 2 was found moving along Shannon Trail nearest its usual territory, while Group 1 deviated toward Van Tyne 13 and then back to the focus of its area.

Observation 69, Apr. 16, 1933, Groups 1 and 2. Had it been possible for me to control the meeting of groups, I could not have arranged a more ideal contact between two clans than that which I observed early this morning. I was following Group 1 as it moved west of Shannon 8 and into the territorial range of Group 2. Suddenly, a blast of roaring howls came from a tree of dense foliage, 25 yards ahead of the leading males. The males of Group 1 became greatly aroused, dashed through the tree tops in double quick time, and roared repeatedly in unison. The adult males moved out from Group 1 and approached nearest Group 2; the females and young came next; and the mothers carrying babies remained in the rear of the column. Group 1 was situated in two trees; Group 2 in an adjacent tree, and the battle of voices was on, with roar after roar recurring irregularly between the clans. The barks of females and the whines of young supplemented the howls of the males. The vocalizations continued for 30 minutes; then Group 2 began progression in a southwesterly direction, and Group 1 reversed its course and moved eastward toward its own territorial range.

These observations, so far as I was able to learn, characterize the relations of clans to each other. A general fact which needs emphasis is that groups rarely come close together. As a rule, one group avoids the others. For each instance of close contact between clans, I observed dozens of instances of groups deflecting or reversing their courses and thus avoiding close contact with another group of animals. Of the cues or stimuli which coördinate the movements of clans and hence their spacing, vocalizations are without doubt the most important. The howls at dawn and in the early forenoon seem to signalize the location of a clan to other near-by ones. Odor may also play a minor rôle. Clans usually tend to avoid stimuli coming from another group, even before the other animals are seen.

I have noted one exception, however, which I shall give here. If Group 2 approached the territory of Group 1 as far as the point between Barbour and Shannon Trails, and Group 1 was located along Pearson Trail, the latter clan would move toward the location of the former. Normally, following several vocal battles, Group 2 would then return to its own territory. There seems to be a tendency for some groups to defend the area to which they are adapted.

I believe it improbable that cross-breeding occurs between groups when they do happen to mingle. The consorts which I saw copulate when Groups 2 and 3 met, were members of Group 2, and I observed them repeatedly afterwards. Howlers tend to avoid strange individuals, and the chances are that if there was an oestrous female in either clan, one of the clan's males would have already become her consort. Inter-breeding among the clans then is apparently carried out entirely by the complemental males as they shift from one clan to another.

The activity of group males is most prominent when two clans meet. The males come near together, and they engage in the inter-group vocalizations. The reactions of one group to another are somewhat comparable to the reaction of clan males to a complemental male. In both cases, vocalizations subserve the function for which pugnacious behavior is fitted. In situations where fighting would occur perhaps with baboons (73) and chimpanzees (49), howler monkeys vocalize. The roaring howl is a defense reaction which occurs in situations where some other animals would fight.

Howler monkeys, as individuals in the clan, do not compete for food, and similarly there appears to be little competition for food among groups. Clans may feed from the same trees but at different times. As one clan approaches the food tree, it may delay until the group then feeding has been satiated and has withdrawn. Competition for food is unnecessary, for there always seems to be an abundance of food in the tropical forest. The present population on the island must increase many times in size before competition for food will become necessary.

The discreteness of howler groups is modified by the vocal intercommunication between them. Through vocalizations, clans stimulate and respond to each other. The barking roars apparently function to coördinate inter-group relations.

The discreteness of groups is also modified by the inter-play among them of complemental males. Some males leave their parental clans, wander independently for a period and then become members of another clan, or perchance rejoin the one from which they came. These complemental males afford a means of bringing about a certain degree of homogeneity among groups which are spatially related.

B. COMPARISONS OF BEHAVIOR AND SOCIAL RELATIONS OF SPECIES AND SUBSPECIES. The data which I have presented are on *A. palliata*. Comparable data for other species of *Alouattanae* are not available. From the literature on the natural history of other species, especially the writings of Azara (5) and Rengger (53), it might be inferred that among the different species a high degree of similarity exists in activities and social relations. To determine precisely what differences are to be found is a problem for further study.

The similarity of behavior and social relations is great among the three subspecies studied in this investigation. By field observations I was unable to detect noteworthy differences between *A. p. aequatorialis*, *A. p. palliata* or *A. p. coibensis*. Their vocal behavior is highly similar, varying no more than individual differences within a subspecies. The three kinds of animals eat the same types of food in the same way. Patterns of locomotion, posturing, and prehension are almost identically the same for the three kinds of animals. The constitutions of groups in *A. p. aequatorialis*, *A. p. palliata* and *A. p. coibensis* were similar, and subgroupings within the clans were the same. So far as my observations indicate, the behavior described in this monograph is characteristic of the species *A. palliata*.

C. SUMMARY. New clans of howlers may be formed by parental clans dividing, subgroupings splitting away from the original group, or by individuals becoming associated with a complemental male. Howler clans may come into close contact, but usually they seem to avoid each other. The howling roar type of vocalization functions as a means of inter-group coördination. Probably cross-breeding among clans is mediated by complemental males. There is a high degree of similarity of activity and social relations among three subspecies of *A. palliata*.

XI. RELATIONS OF HOWLERS TO OTHER ANIMALS OF THE SAME ENVIRONMENT

After describing the social relations of individuals and groups of howling monkeys, descriptions are pertinent of the relations between howlers and other classes of the native fauna. It is most important to know something of the interactions between howlers and other primates. It is also desirable to know what predatory animals may be found.

A. RELATIONS WITH VULTURES AND HAWKS.

Observation 70, Jan. 5, 1932, Group 1. I was observing Group 1 at Barbour 2 when suddenly the entire clan was thrown into an uproar by a flock of black vultures (*Catharista Urubu*). The birds flew swiftly into the midst of the group and seemed to be fighting among themselves. They lit in the same trees with the group of monkeys, and as they did so a burst of howling roars was given; young monkeys dashed for their mothers which took them on their backs; and the males rushed toward the birds roaring furiously. No sooner had the birds perched than they took to the air again, and one of them dropped the hind leg of a sloth which had apparently been dead for several days. The defensive roars of the howlers continued for about ten minutes and then the animals began feeding.

Observation 71, Feb. 25, 1932, Group 2. For more than four hours I observed Group 2 as it fed and rested near the nest of a Geisbreck's hawk (*Leucopternis ghiesbreghti costaricensis*). The young animals played while older animals fed, without their behavior being diverted in the least by the presence of the formidable bird, which might easily have attacked an infant howler which had strayed away from its mother.

Although there is a possibility that some large hawks may capture infant monkeys, the evidence would not support such an inference. (Chapman informs me that there is a monkey hawk in Africa.) Only in the above instance have I seen howlers react defensively toward large birds. Howlers and guans (*Penelope cristata cristata*) as well as howlers and toucans (*Rhamphastos swainsonii*) frequently feed together from the same trees.

B. RELATIONS WITH COATIS. I have seen howlers and coatis on several occasions feed from the same tree at the same time (usually a *ficus* tree), but seldom have I seen them so intimately associated as the following observation describes.

Observation 72, Jan. 23, 1932, Group 2. Group 2 was feeding in a fig tree with eight or ten coatis (*Nasua narica*). Young howlers approached these animals, swung down toward them, and grasped at their tails and fur. The coatis withdrew and the young monkeys chased them. Finally the coatis took to the ground and escaped. Apparently the approach of even juvenile howlers is sufficient to cause coatis to show avoidance reactions.

C. RELATIONS WITH OCELOTS AND OTHER LARGE CATS. General opinion of persons acquainted with Central and South American fauna holds that large cats, ocelots, pumas, and perhaps jaguars, are enemies of monkeys. There is no evidence of which I know of jaguars attacking monkeys. My companion, "Mexico," reports in a dramatic and sincere manner his observations of a puma luring white-faced monkeys to the lower branches of a tree and then jumping and catching them. Clark tells me of seeing capuchin monkeys reacting defensively toward a female ocelot which had two kittens. It is possible that the semi-arboreal ocelots occasionally attack and catch infant howling monkeys. It was my good fortune to make one observation relative to the possible relations of ocelots and howlers.

Observation 73, Jan. 2, 1933, Group 2. I was searching for Group 2 along Shannon Trail from no. 6 to no. 10 early one morning. I was listening for sound cues, when the distress cries of a young howler burst forth twenty yards from me followed by the continuous roars of several males. I hurried toward the sounds. As I approached, a dark, cat-like form came down an inclined corozo palm tree to within ten feet of the ground, jumped and ran away through the forest. Among the branches of this same tree I saw a juvenile howler which later moved out on a branch where I could observe it closely. Great drops of blood fell from the young animal and splattered on the leaves below. After sitting quietly for a few minutes, the juvenile moved slowly away with the clan.

The group males were apparently about the distance of two tree tops away when the attack occurred, and when I saw them they were rushing toward the place where I later located the juvenile and from which the cat-like animal was moving. They were roaring as I have rarely heard howlers roar.

I interpret these observations to the effect that an animal, which I am convinced was an ocelot, had climbed an inclined palm tree, crouched among the fronds and attacked a juvenile howler which came near it. The cries of the juvenile stimulated the defensive reactions of the males. The roars of the howlers caused the ocelot to withdraw, but not before it had inflicted a deep, bleeding wound on the juvenile animal.

In my opinion, an attack by an ocelot like that just described is a very rare occurrence and the attempt of the cat to attack and catch a young howler is probably frustrated more often than not by the clan males, just as was the case in the observation listed. The high degree of cohesiveness in howler clans assures the presence of adult males near young animals. The roars and apparent viciousness of the males will, in all probability, frighten away an ocelot.

I have observed places on stones, leaves, and fallen tree trunks where blood had been spilled. In some instances, the blood was rather fresh, in others it had dried brown. Since I could discover no marks, tracks, or other cues indicating that an animal had been on the ground, I inferred that the blood came from an arboreal animal, probably a howler.

I have found the skeletal remains of only two howlers during the relatively long periods that I tramped the forests of Barro Colorado Island. In both instances, the bones and skulls were those of early juvenile animals.

It is extremely difficult to make observations on the relations of pumas to howlers. Pumas are rarely seen by man, but the two which I have seen were not behaving with reference to howler clans in any way. Since pumas are terrestial in the main and probably find an abundance of food, especially small mammals, on the ground, I doubt if they attack arboreal howling monkeys.

D. RELATIONS WITH OTHER SPECIES OF PRIMATES. In the section on procedures I have discussed the reactions of howlers to man. No doubt man is the monkey's greatest enemy. Natives kill them for food, for their skins, and for sport. The effects of their being hunted can be readily observed when the sparseness of the howler populations and smallness of clans are noted in areas where they are hunted, e.g., near Puerto Armuelles, around the camps on Coiba Island, and on the mainland of the Canal Zone. These figures should be compared with those for regions like Barro Colorado Island, which is strictly protected, or places which are uninhabited by man, like the west and southwest parts of Coiba Island or the Coto region. In howler populations protected from indiscriminate hunting, apparently the numbers of animals will be limited by the lack of food or epidemics of some disease. (The bot-fly, *Cubereba baeri* Shannon and Green, may cause some deaths.) Howlers are not hunted by natives as are some other monkeys, because they are not as desirable for pets. However, many are killed.

1. Relations with capuchin monkeys. The following examples of observations illustrate the relations between howlers and capuchins (*Cebus capucinus*).

Observation 74, Jan. 25, 1932. While a clan of howlers was feeding on figs, a band of capuchins came and fed from the same tree. There was no aggressive behavior nor was antagonism evidenced. The howlers continued to eat and the capuchins plucked a few figs, ate them, and moved quickly away.

Observations 75, Feb. 4, 1932, Drayton 4. A band of capuchins came into the same adjacent trees with a group of howlers. For twenty minutes the animals of these two species fed and played on the same trees, but so far as I could observe, they never reacted with reference to each other. Howlers do not repulse capuchins, but just as certainly there is no affinity between the two species.

Observation 76, Apr. 26, 1932, Groups 13 and 14. Groups 13 and 14 were closely associated, and scattered among the howlers were capuchin monkeys. Vocalizations other than those characteristic of the two species during progression were not heard. No inter-species antagonism was observed. The lack of even temporary association between these animals is, in part I believe, due to differences in the type and rate of locomotion.

Observation 77, Jan. 21, 1933. A band of capuchins was feeding between two large groups of howlers, and later the capuchins passed through howler Group 16. Between the different species there were no behavioral interactions.

The reason why howlers and capuchins are not reactive in a close way is fairly clear. In the first place, they eat different kinds of food in the main, although there is some overlapping in the foods preferred. Competition for food is, however, eliminated as a source of strife. Secondly, the degrees and kinds of nomadism characteristic of the two species differ greatly. Howlers are slow movers, whereas capuchins are rapid travelers; howlers travel for short distances and cover a relatively limited territory, whereas capuchins may cover twelve or fifteen hundred yards without stopping and range over a relatively large area; the reactions of howlers are slow, those of capuchins are rapid. There is no affinity between the two species because of very diverse reaction tendencies. Reciprocal social activity, such as play or sexual behavior, is improbable between individuals of these two species in a free range. Without interrelated action patterns, reciprocal social conditioning does not occur. Nevertheless, the animals are rather frequently associated for short periods, but conflicts of any consequence apparently do not occur.

Capuchin monkeys, especially complemental males, may at times be observed traveling for hours with a group of red spider monkeys (*Ateleus geoffroyi* Kuhl), but I have never observed an animal of another species closely associated with a group of howlers except "accidentally," and I have never seen a howler associated with a group of another species. Although within the limits of a particular section of the Coto region in 1933 several howler groups lived among many red spider groups, I have never seen reciprocal behavior between them. However, single male capuchins were seen associated at times with red spider groups. There are close similarities in the food eaten and in the type and rate of locomotion of spider and capuchin monkeys.

The night monkey (*Aotus zonalis*) and the marmoset (*Oedipomidas geoffroyi*) have never been seen associated with howlers. Pairs of night monkeys live in hollows of trees during the day and feeding is done at night; hence their characteristic diurnal cycle of activity would preclude their association with howlers. The marmoset prefers low scrub forests as a habitat, a type of forest into which howlers rarely go; hence these two species come into contact very infrequently.

E. SUMMARY. The relations of howling monkeys to the fauna of their habitat have been discussed. Man and ocelots seem to be the most serious enemies of howlers. Ocelots infrequently may attack and kill young howlers. Neither howler individuals nor groups associate closely with other monkeys of the same region. When howlers and capuchins are thrown together, there are few specific behavioral interactions between them.

XII. GENERAL SUMMARY

In this study of the behavior and social relations of howling monkeys an attempt has been made to contribute to a comprehensive psychobiological study of primates. I have sought to present observations with as much objectivity and as little theorizing as possible.

About eight months were spent studying howling monkeys in the Panama Canal Zone and in the Republic of Panama. Carefully planned observational procedures were used to investigate the behavior of *A. p. aequatorialis*, *A. p. palliata*, and *A. p. coi-*

bensis. The following generalized statements summarize the findings on these monkeys:

Howlers may behave neutrally toward an observer, they may react defensively or bluffingly, or they may flee and conceal themselves. Apparently the type of reaction shown depends in part on the previous conditioning of the animals. While behaving in a defensive, aggressive manner toward an observer, they may drop objects with reference to him.

The hands show a concentric type of movement toward the palmar surfaces in manipulation, and there is a functional division between the first and second digits. The thumb is not opposable to the other digits. The tail is prehensile and is used almost constantly.

Howlers show considerable variability in posturing during rest, locomotion, and feeding.

Locomotion is typically pronograde with few variations toward an orthograde form. Howlers are awkward in locomotion on the ground. They can swim if necessary.

Howlers feed from the terminal twigs of trees and as a rule pull in with their hands the stems containing the food and eat directly from them. In food preference, they are herbivorous and frugivorous, but primarily the former.

Groups of howlers tend to occupy a definite and limited territory. This region may be shared with other groups and there occurs from time to time some shifting of territorial range. Within their territories groups behave with reference to food and lodge trees. The groups travel at the average rate of about one hundred yards per hour and seldom move more than eight hundred yards per day. The groups move in an irregular column. There is a strong tendency for males to lead the groups and for females carrying infants to travel in the last positions of the column.

Howlers prefer dense, tall primary forests as a habitat and apparently avoid scrub growth.

As determined by carefully made censuses, there were 398 ± 50 howlers on Barro Colorado Island in April, 1932, and 489 ± 25 individuals in April, 1933. The means and standard deviations for the 23 groups counted in 1932 are 17.3 ± 6.8, and for the

28 groups of the following year 17.4 ± 6.8. There were, in both years, 18 animals in the median groups. The groups ranged in size from 4 to 35 individuals in 1932 and from 4 to 29 animals in 1933.

The groups vary in size and constitution from time to time as young are born, as individuals, especially males, join or leave the clan, and as animals die. The composite mean grouping tendency for the howler groups of Barro Colorado Island equals (M 2.8 ± 1.2) + (f4.8 ± 2.5) + (m 2.4 ± 1.5) + (i1.7 ± .7) + (i2 1.4 ± 1.2) + (i3 1.2 ± 1.4) + (j1 1.3 ± 1.0) + (j2 1.8 ± 1.2) + (j3 1.0 ± 1.1) + (M_IX). The proportional composition of groups in percentages equals (M 16.4) + (f 27.3) + (m 13.5) + (i1 4.1) + (i2 8.0) + (i3 7.1) + (j1 7.6) + (j2 10.5) + (j3 5.5) + (M_IX).

The socionomic sex ratio of adult howlers is approximately 28 per cent males to 72 per cent females.

Within groups there are subgroupings.

Females clean their infants after birth and eat the amniotic fluids.

Mothers carry infants first on their bellies and then on their backs in the sacral and lumbar regions. In general, the infants behave parasitically to the mothers, which are relatively indifferent to them. However, mothers may at times posture for their young to mount them, help the infants over critical crossings, and retrieve young ones when they fall. The social relation between a mother and her infant is a specific one.

The strength of the female-young bond rises and then declines as the infant grows older. About the time of weaning the mothers may even mildly fight their young. Early juveniles continue to associate with their mothers after a sibling is born.

The relations among females of a howler clan are peaceful and communal.

The amount of play shown by young howlers increases until the juvenile 1 stage, and then there is a rather sharp decline to a minimum of play in adult animals. Several rather stereotyped forms of play are shown by young howlers, but especially noteworthy are the wrestling and chasing play patterns.

Female howlers show a rather definite oestrous period during which primary sexual activity occurs frequently. Copulations may occur as frequently as every ten or fifteen minutes during the oestrous period of the female, but there may be several hours between copulations. For 19 copulations the period of adjustment was 9.7 ± 5.7 seconds; the period of intromission in 25 instances was 21.8 ± 2.8 seconds, and the number of thrusts averaged 16.9 ± 4.8.

Characteristically, prior to copulation a female howler postures and rhythmic tongue movements are exchanged between her and the male. Copulation typically occurs with the male mounting the female. During the oestrous period of a female, a male associates very closely with her as a sexual consort until he is sexually satiated, and then another male may take his place. The data indicate that males mate communally with an oestrous female, but they do not show whether particular males consistently become consorts prior to other males.

Howlers reproduce throughout the year, but the frequency of births may vary from season to season. The observations suggest that there is a higher per cent of infants 1 in the clans in January than in any of the following four months.

In general males behave indifferently to young animals, but they may assist in retrieving fallen infants, protect them from predatory animals, and in unusual situations care for an infant in somewhat the same way as a mother.

The males of a howler clan behave coöperatively in leading and defending the group. Pugnacity and competition among integrated clan males were not observed. Clan males behave toward a complemental male which approaches a group as if he were an enemy.

How complemental males come to separate from clans is not known, but these animals, which live temporarily separated from groups, again become parts of a clan either suddenly or by a long process of social adaptation.

The males are dominant in controlling and coördinating the clan. Contact control and distant signalization subserve group coördination. Posturing, gesticulation, and vocalization are important kinds of distant signalization.

Nine different patterns of vocal behavior were described in this report, although many more actually occur. These patterns vary greatly in the specificity of their stimulating situations and in the specificity of responses stimulated in associated animals. The barking, roaring type of vocalization functions as a means of defense and inter-group control.

New clans may be formed by parental clans dividing, by individuals of a group joining a complemental male, and probably most frequently by subgroupings separating from the parental clan. Groups of howlers when they come near each other engage in vocal battles. Apparently two groups rarely, if ever, become consolidated.

Inter-breeding between groups which are relatively discrete societies occurs through the exchange of complemental males.

The literature and the observational data of this report indicate that there is a high degree of similarity in the behavior and social relations among the different subspecies of howling monkeys. Data on three subspecies of *A. palliata* suggest that the behavior and social relations described in this monograph may be characteristic of the entire *palliata* group.

The indications are that man is the most serious enemy of howlers and that occasionally young animals may be attacked by ocelots.

Howlers are not commensal with any other species of primate living in the same environment. Capuchins and howlers may, however, feed from the same trees for short periods of time.

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PLATES

PLATE 2

A. Aerial view of Barro Colorado Island.
B. Aerial view of the "Laboratory" and surrounding area.
(Photographs by U. S. Army Air Service, France Field, Canal Zone.)

PLATE 2

PLATE 3

A. View of the "Laboratory" from the lake.
B. Our camp in the Coto region of Northwestern Panama.

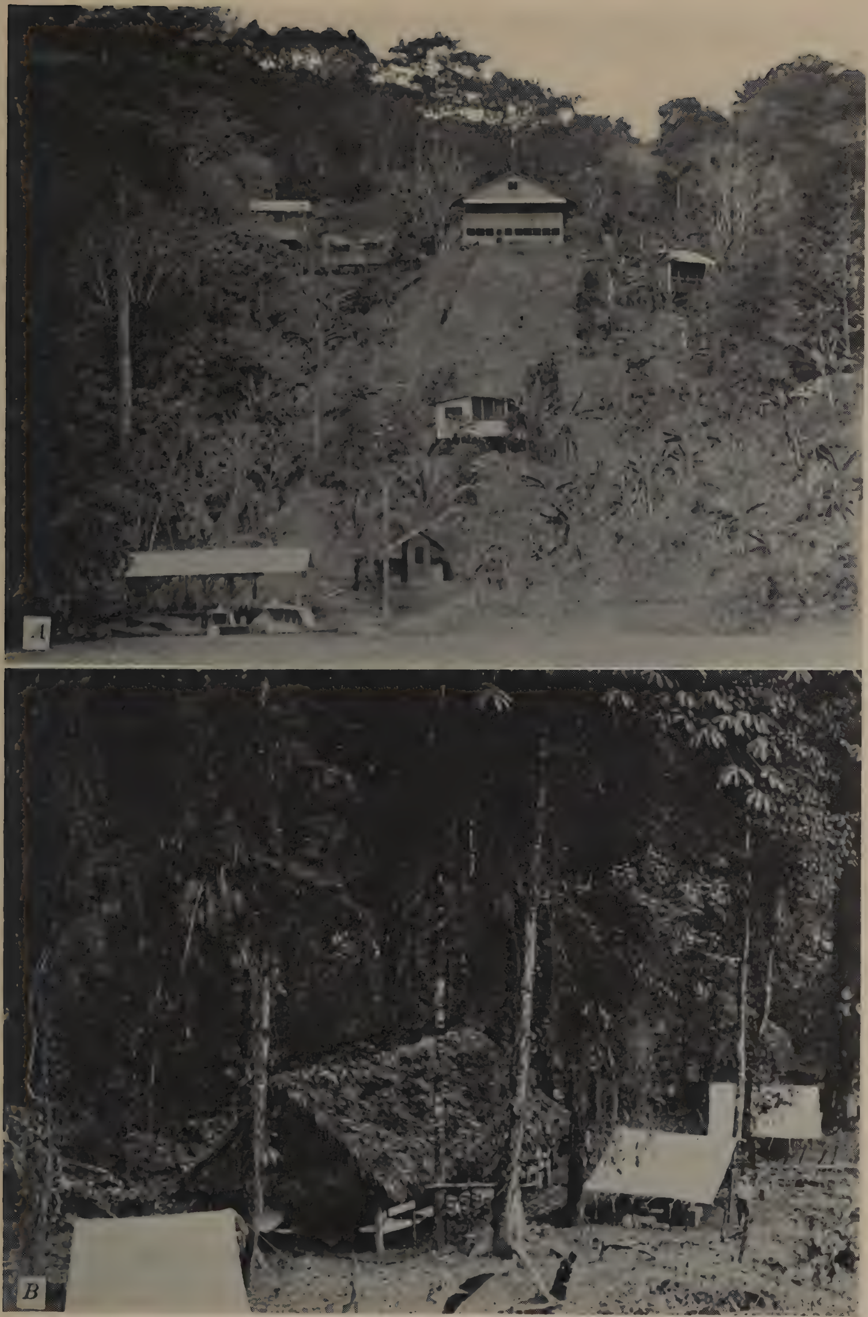


PLATE 3

PLATE 4

A. View of the Barro Colorado Island forest from the lake.

B. View across Gatun Lake including the channel of the Panama Canal taken from the "Laboratory."

C and D. Views of the La Vaca River and bordering forests in the Coto region.

PLATE 4

PLATE 5

A. Portrait drawing of the face of an adult male howler. (Drawn from a photograph by Willard E. Moore.)

B. Portrait of an eleven months old male howler.

A

B

PLATE 5

PLATE 6

A. Part of Group 1 resting in an acacia tree.

B. A subgrouping consisting of an adult male, an adult female, a juvenile 1, and an infant 2. (Photograph B by Ottis E. Shattuck.)

PLATE 6

PLATE 7

A and B. Part of Group 1 feeding in an acacia tree. Note feeding postures.

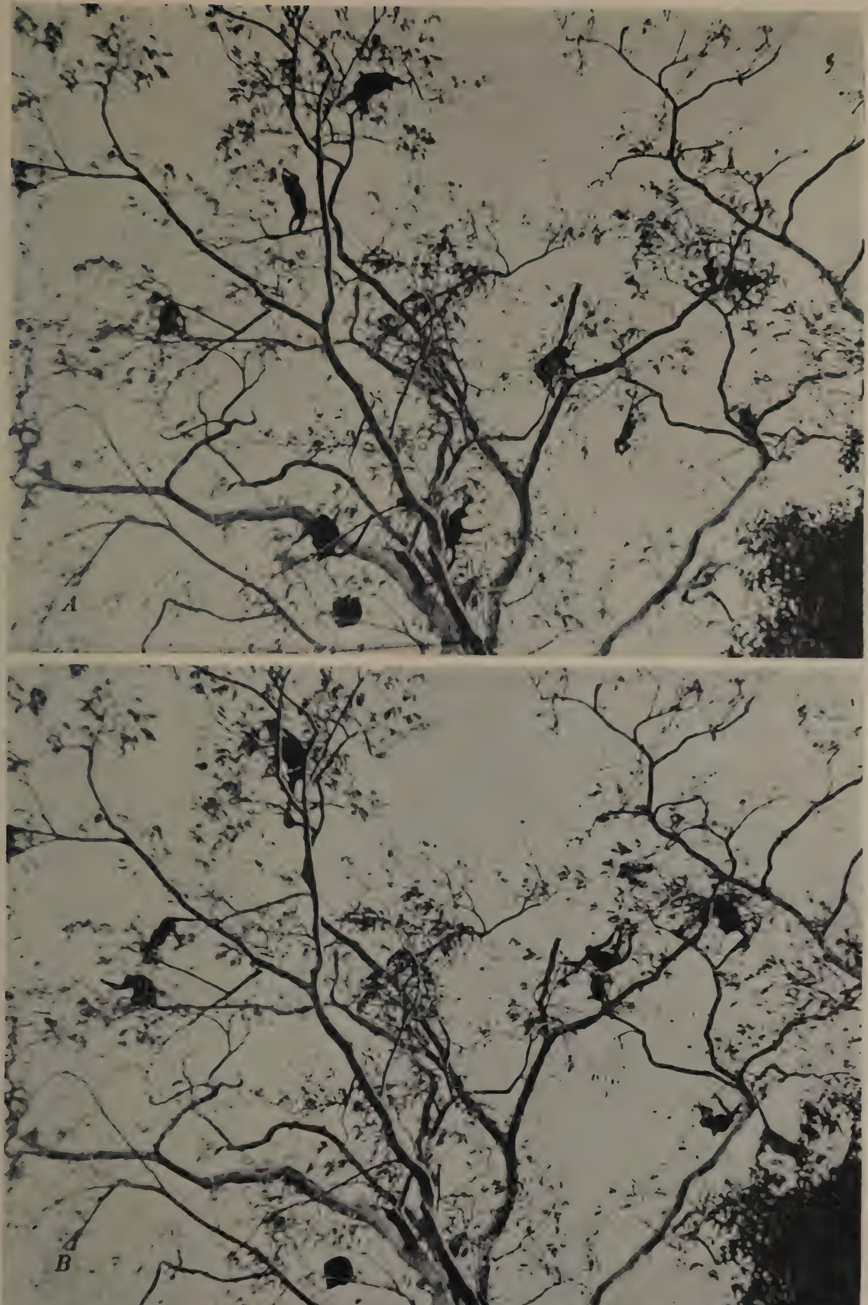


PLATE 7

PLATE 8

A. A young adult completing a critical crossing upward from *a* to *b*.

B. A young adult in a posture preparatory to jumping downward over a critical crossing from *a* to *b*.

C and D. Feeding activity in howlers.

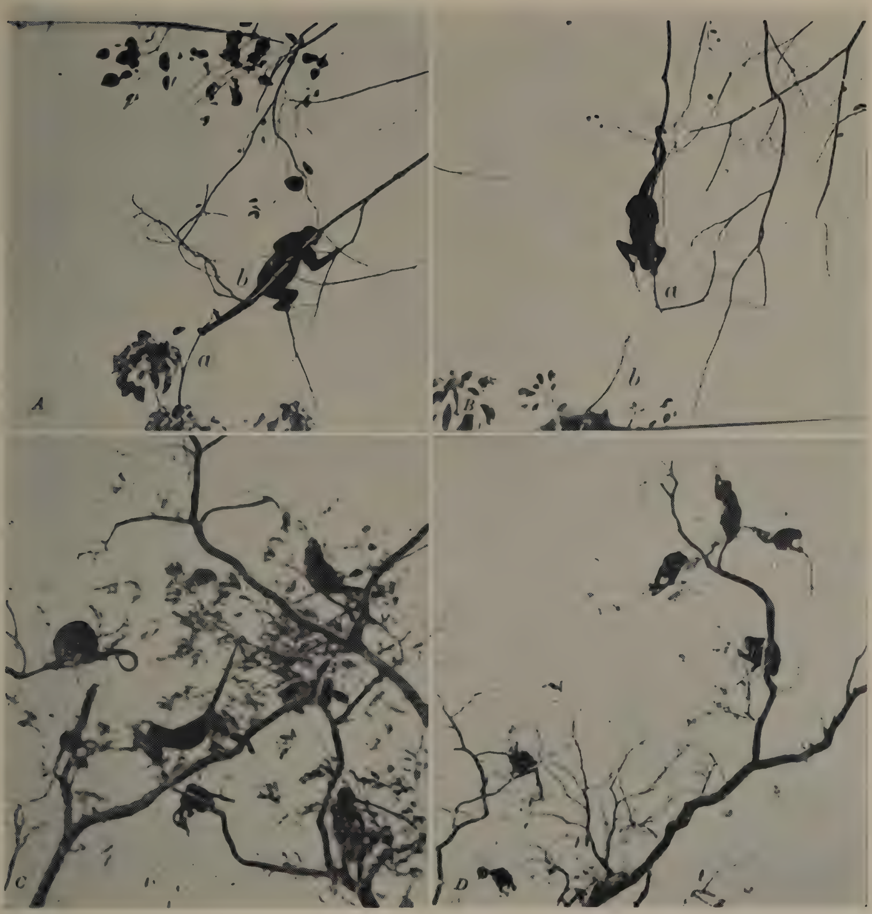


PLATE 8

PLATE 9

A. An adult male howling at the observer.

B. An adult male at rest. Note scrotum.

C. A female reacting to her fallen infant and to the observer. A male and a juvenile 1 are in the background.

D, E, F and G. Adult males at rest.

H and I. Adult males feeding.

PLATE 9

PLATE 10

A, B, C and D. Adult females at rest.
E and F. Adult females during locomotion.
G, H and I. Females and young at rest.

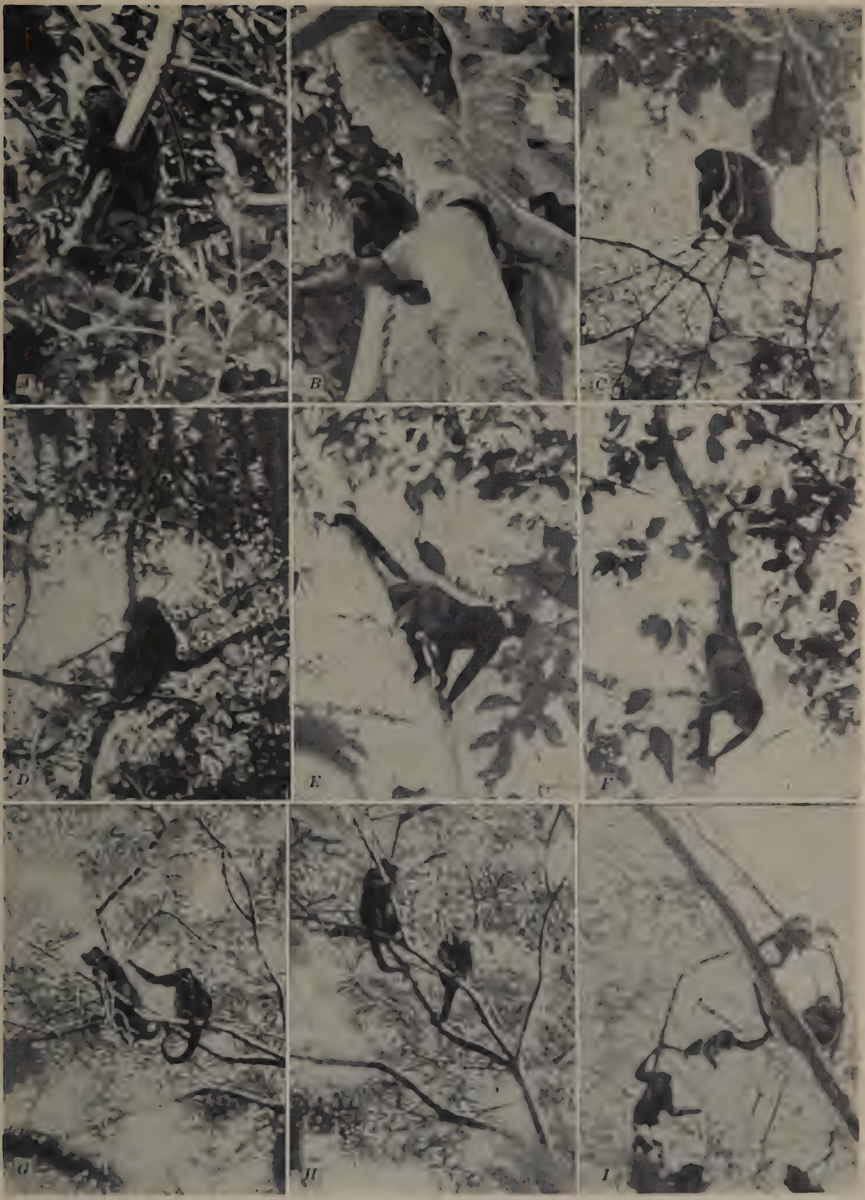


PLATE 10

PLATE 11

A. Male and female sexual consorts at rest. Note the proximity of the pairs in all photographs on this page.

B. The same pair during locomotion.

C. Primary sexual activity in the dorso-ventral position.

D. A male following an oestrous female in a typical manner.

PLATE 11

PLATE 12

A. An adult female.
B. Female carrying an infant 1 on her belly.
C. Female carrying an infant 1 on her side.
D. Female carrying an infant 2 on her back.
E. Female and infant 2 at rest.
F. Female posturing over an infant in a defense situation.
G. Female carrying an infant 2.
H. A female, an infant 1, and a juvenile 1 forming a subgrouping.
I. An adult female.

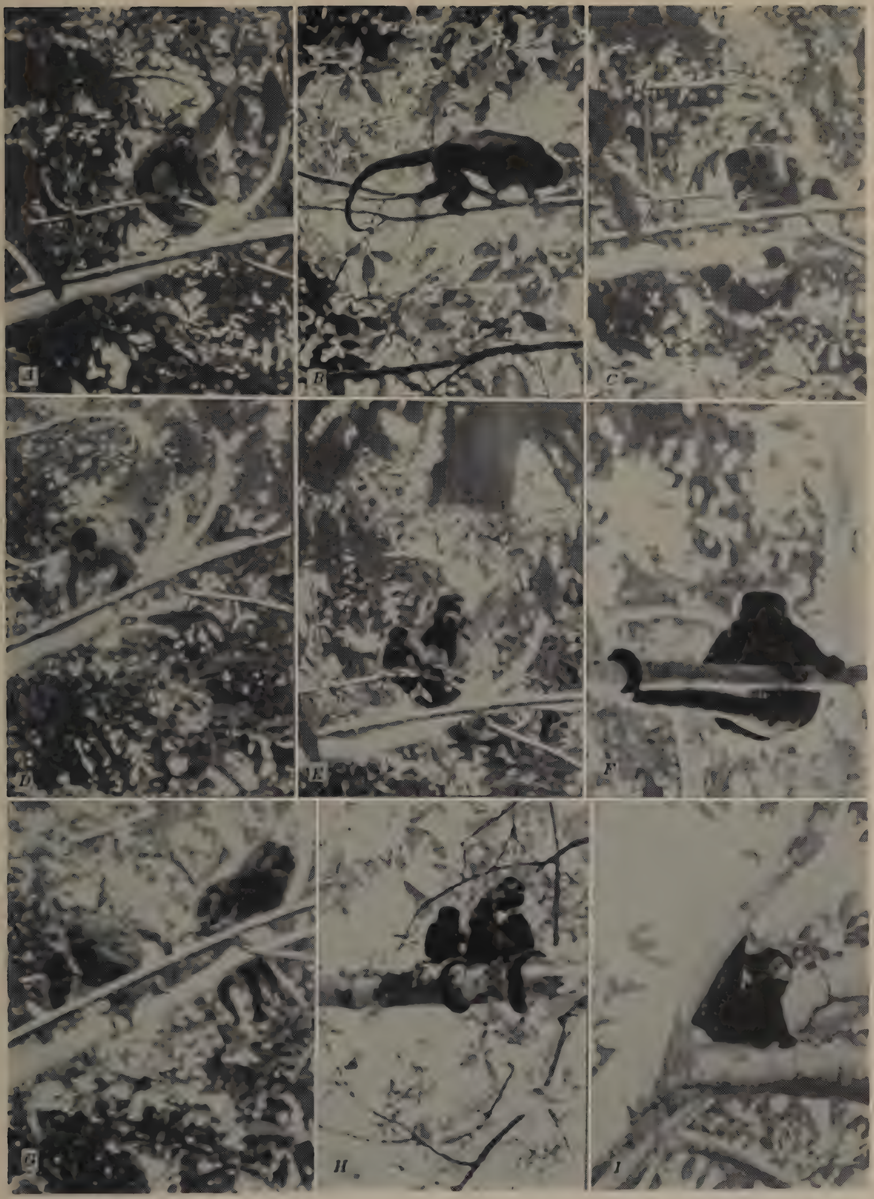


PLATE 12

PLATE 13

A. A female making a critical crossing with an infant 2 in a typical position.

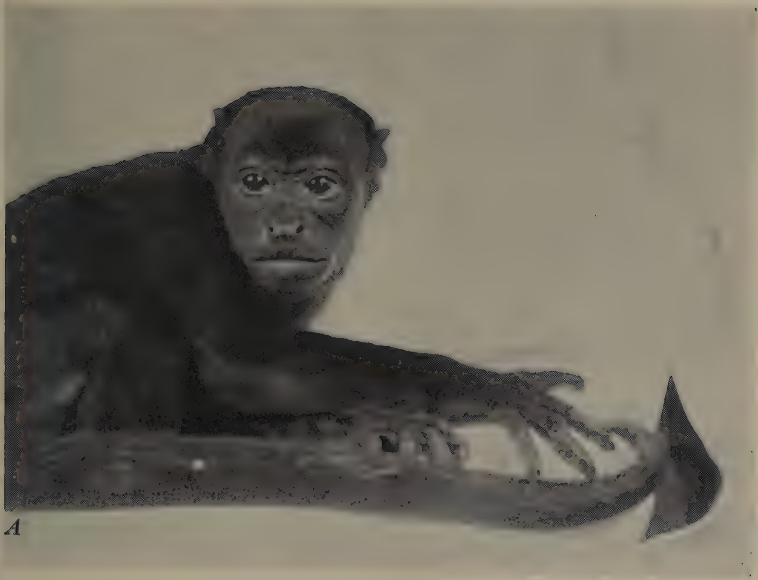
B. An infant 3 completing a critical crossing after its mother had formed a bridge for it with her body.

PLATE 13

PLATE 14

A. "Juanito," an eleven months old male howler. Note the division of the fingers.

B. "Chipper," a twelve months old red spider female (*Ateleus geoffroyi* Kuhl), and "Juanito." This had been the typical resting and sleeping position for the infants during the thirteen months of their association.



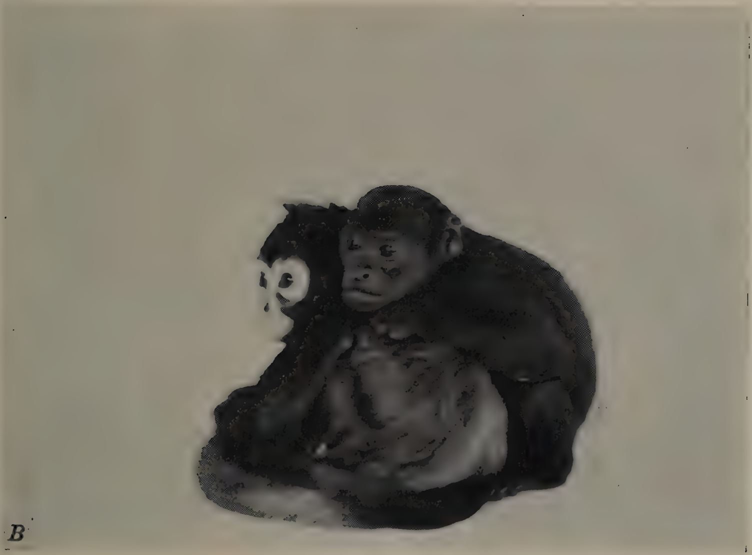


PLATE 14

PLATE 15

A, B, C and D. Photographs of an infant howler approximately two weeks old. Note light grayish color and the division of the fingers of the left hand in B.

E. The same infant when about two months old. Compare size with photograph H taken six weeks earlier. Note change in color.

F. An infant 1 walking on a flat surface.

G. An infant 1 on its favorite support.

H. An infant 1 giving its distress cries.

I. "Juanito" and "Chipper" at about two and three months of age respectively.

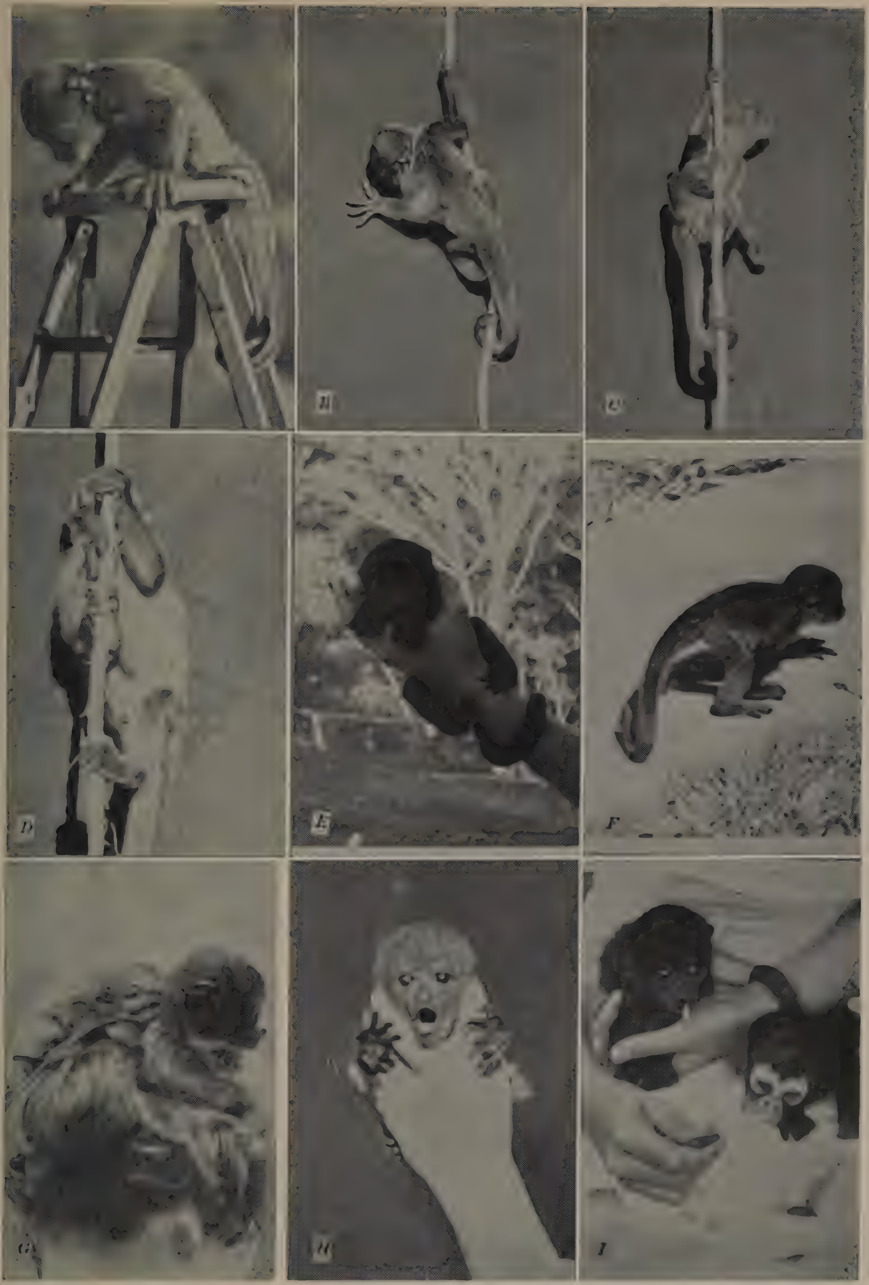


PLATE 15

PLATE 16

A. A young howler badly infested with bot-fly larvae (*Cuterebra baeri* Shannon and Green).

B. Hind feet of a juvenile howler.

C, D and E. External genitalia of oestrous females showing lack of swelling.

F. External genitalia of an adult male.

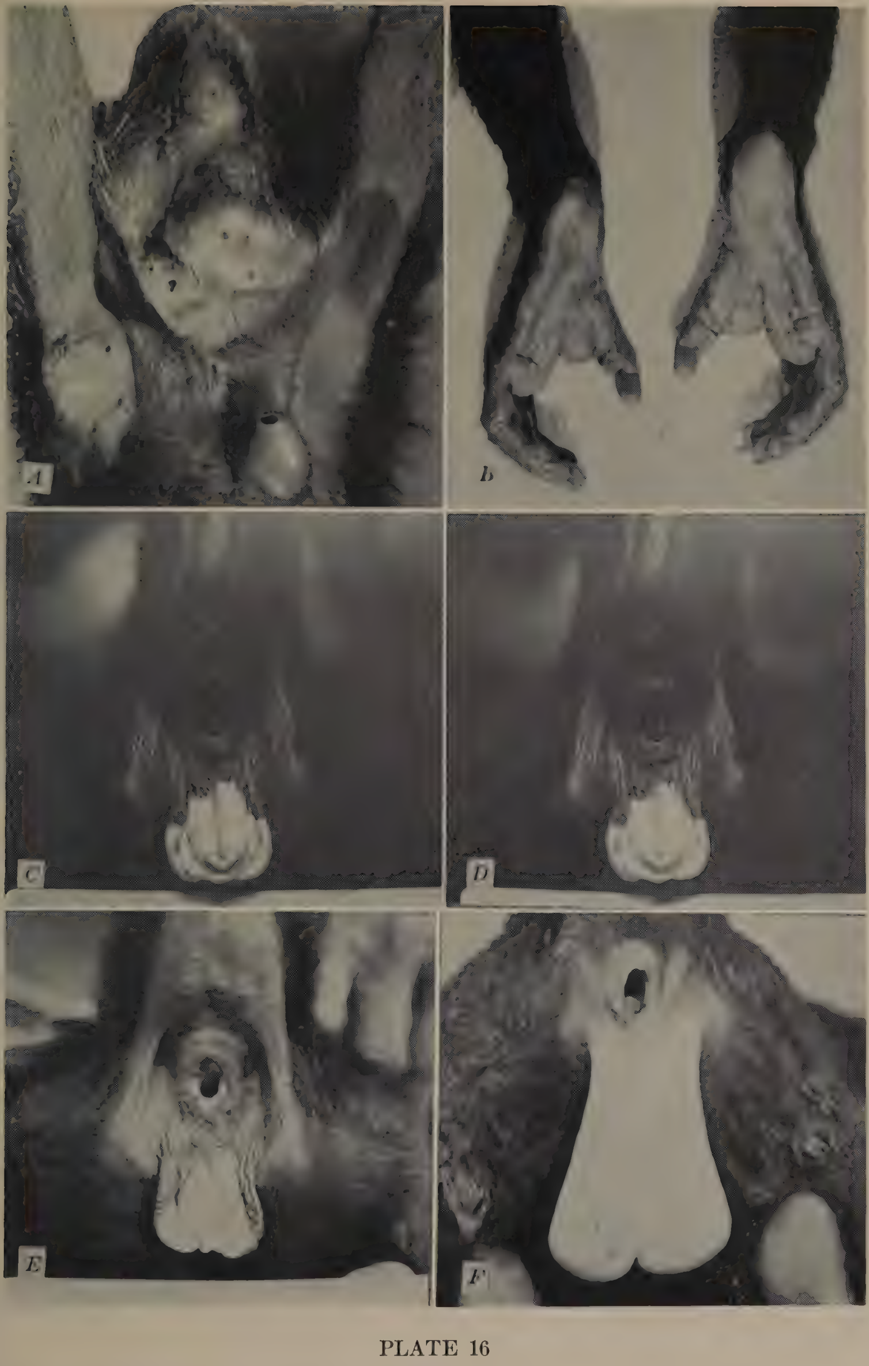


PLATE 16

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AUDITORY ACUITY OF MONKEYS

BY
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AUDITORY ACUITY OF MONKEYS

G. R. WENDT

Laboratory of Neurophysiology, Yale University School of Medicine

So far as the writer is aware, no data on the auditory acuity of monkeys have been published. The data on primates are limited to papers on the auditory acuity of humans and the recent paper of Elder (2) on the auditory acuity of the chimpanzee.

The data reported in this paper represent the first stage of a program of research undertaken in collaboration with Dr. J. G. Dusser de Barenne on the functional localization of the auditory mechanisms in the cerebral cortex of monkeys. At this time results are being presented on the auditory acuity of five monkeys (one macacus, one baboon, one mangabey and two spider monkeys) as shown by their intensity limens for pure tones of frequencies from 64 to 16,384$\sim$. The determinations, made in an open sound field, are compared to the limens of a group of human subjects tested under similar conditions.

I. METHOD

The animal was confined in a cage with a barred aperture (grille) through which it could reach out to open a drawer containing a piece of food. The grille could be closed by a curtain. The animal was so trained that at the opening of the curtain it took up a position in front of the grille and waited for the occurrence of the tone which was the signal for opening the drawer. The index of hearing at any trial was therefore the act of opening the drawer during the duration of the tone. Figures I and II show the arrangement of the parts of the apparatus.

Apparatus

A complete discussion of the requirements of auditory apparatus is in preparation as one chapter of a monograph on conditioned reflex apparatus and procedures. This description will therefore be limited to a brief summary of the essential features of the apparatus used in the present experiment.

1. *General arrangement.* The experiments were conducted in a sound-shielded room. Figures I and II show the arrangement of apparatus. It will be seen that the room is partially divided by a baffle into two compartments of unequal size. The experimenter occupies the smaller compartment, and the animal cage occupies the larger one.

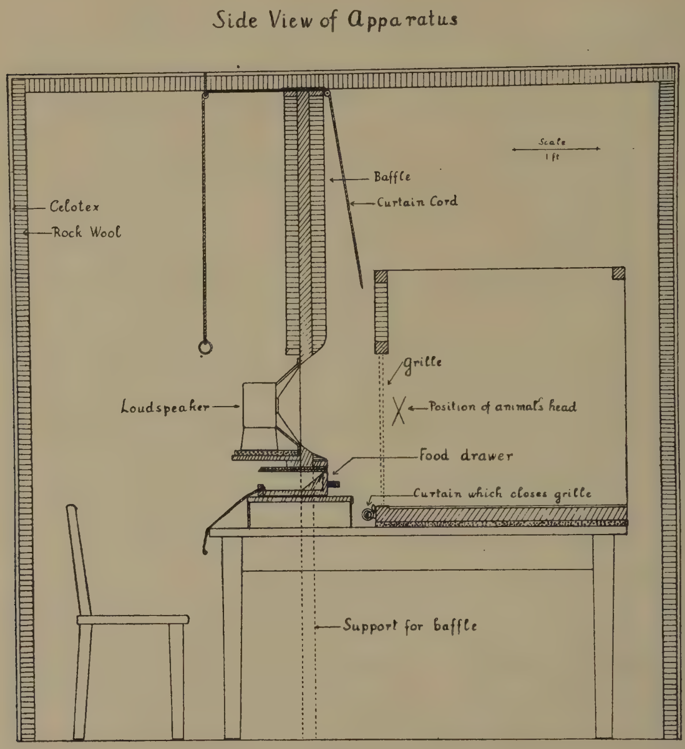
Side View of Apparatus
Scale
1 ft
Baffle
Curtain Cord
Celotex
Rock Wool
Grille
Position of animal's head
Loudspeaker
Food drawer
Curtain which closes grille
Support for baffle

FIG. I

2. *Sound-shielded room.* The experimental room was designed to exclude external noises. Inside dimensions are approximately 6′ x 8′ x 8′. The walls are built up of two separate walls of

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gypsum block with plaster on the inner and outer surfaces, making a total thickness of 12 inches. The room is built into one corner of a larger room whose walls and ceiling are covered with 1 inch Acoustic Tile. The outer surface of the sound-shielded room is similarly covered. Two heavy doors close the opening of the room tightly enough to prevent direct sound leakage.

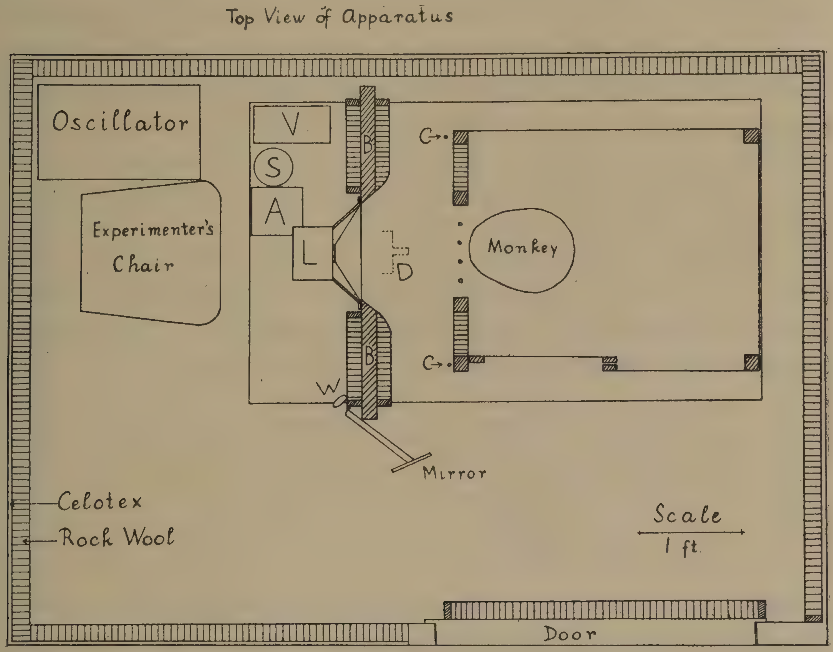
Top View of Apparatus
Oscillator
V
S
A
L
B
B
Experimenter's Chair
D
Monkey
C
C
W
Mirror
Celotex
Rock Wool
Scale
1 ft
Door

FIG. II. *B*, loudspeaker baffle; *D*, food drawer; *L*, loudspeaker; *V*, voltmeter, *S*, saline switch; *A*, attenuator; *W*, stop-watch; *C*, curtain cords.

This room is quite satisfactory for the exclusion of air-borne noises. However, noises such as those of slamming doors, hammering, and so on, which are communicated through the walls of the building, are not significantly reduced because the room is constructed as an integral unit with the floors, walls and ceiling of the larger room, with no provisions for its isolation from sounds arriving by way of conduction through the foundations. But since such noises are almost always intermittent, their effect on the animals is only rarely that of masking the tone stimuli or interfering with response.

3. *Acoustic treatment of interior of room.* When a tone is produced in an enclosed space, a large fraction of the energy incident on the walls is reflected. This reflected sound forms interference patterns which result in "standing waves." These regions of maxima and minima may amount to differences of several hundred per cent in physical intensity, and become troublesome sources of variability in the stimulation strength at the animal's ear. Furthermore, the coincidence of such a region with the sounding source (the loudspeaker) may reinforce or impede its action greatly. Such factors will not operate as constant factors, since a slight shift in frequency or in the position of the animal will change the standing wave pattern. To minimize this factor the walls and ceiling of the room and both sides of the baffle were covered with a highly sound-absorbent material (Johns-Manville Rock-Wool, their "Banrock" blankets). The absorption efficiency of this material is as follows (1):

Frequency	*Per cent energy absorbed*
128∼	66
256	74
512	84
1024	88
2048	80

Strictly comparable figures for other frequencies are not available, but measurements by another laboratory show the efficiency at 4096∼ to be about the same as at 2048∼. The Rock Wool is applied over $\frac{1}{2}''$ celotex, which probably gives additional absorption capacity. The floor of the room is cork tile. Under such conditions interference patterns should be relatively inconspicuous. No instrumental test of the uniformity of the sound field has been made, but both from subjective impression and on the basis of the uniformity of the performance of the animals, we get the impression that the situation is satisfactory.

4. *Tone source.* An electro-dynamic loudspeaker of the direct radiator type with a 12-inch cone was secured from the Jensen Radio Manufacturing Company, Chicago, Illinois. It is their

M20–3405A auditorium speaker. The field coil excitation supplied from storage batteries, was kept at 3.5 ±0.1 amperes. The advantage of using such a large speaker as this one is in the comparative absence of distortion and of harmonic frequencies when it is operating at levels far below its capacity. The cone of the speaker is protected from the animal by wire screening.

As a source of alternating current to drive the loudspeaker a General Radio Company 613-A (serial No. 51) beat-frequency oscillator (General Radio Company, Cambridge, Mass.) was used. This delivers sinusoidal waves of frequency up to 20,000 c.p.s.[1] with 3 per cent or less harmonic distortion and accuracy of frequency setting within 2 per cent.

5. *Control of tone intensity.* The output of the oscillator was set at 0.5 ±0.02 volts as measured by a General Radio type 483-C meter. The intensity adjustment was by means of calibrated resistances, the General Radio type 529 attenuation network box or audibility meter. This device is calibrated in decibels (db), the now generally accepted unit of audibility, and gives a total reduction of 60 db in steps of 2 db. An additional 60 db of attenuation was secured when necessary by an auxiliary attenuator constructed of two General Radio type 500 resistors. With this arrangement the limens of hearing were reached by introducing from 4 to 90 db of attenuation, the figure varying with the frequency used.

Note: The decibel is a logarithmic unit which gives an expression of the ratio of voltage or power input to output. A change of 1 db represents a tone intensity change which is approximately the minimum change necessary to obtain a perceptible difference in sensation (1 db = approximately 1 j.n.d.). Actually the differential limen is sometimes a little more, sometimes a little less than the decibel, depending on the frequency and the location in the auditory area. For a discussion of the relation of the decibel to loudness steps see Fletcher (3).

6. *Control of onset of tone.* The click which accompanies the onset of a tone when the circuit is suddenly completed was elim-

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[1] c.p.s. = cycles per second.

inated by a simple device invented by Professor Raymond Dodge (personal communication). Across the leads between the oscillator and the attenuator is placed a short-circuiting saline-solution switch. This switch consists of a glass beaker filled to within 15 mm. of the top with saline. Connected with one oscillator output lead is a large electrode submerged in the solution; connected with the other lead is a platinum pin dipped into the solution. So long as the pin is in the saline a large proportion of the current is short-circuited. If the pin is held against the side of the beaker and slowly withdrawn, maintaining contact with the glass, it draws up with it a bridge of saline which becomes thinner as the point is raised. In this way the short-circuit is removed gradually, and a smooth onset of tone results. The pin is lifted from the saline by a pendulum which gives a build-up period of 0.05 second. In the critical series of experiments the pendulum was manually released. The pendulum bob is held at one end of its swing by a magnet. The experimenter places the finger tip against the bob. At the time for the stimulus a very slight increase of pressure is sufficient to release the pendulum and ($\frac{1}{2}$ seconds later) lift the electrode out of the saline. There are no secondary cues attending the operation of this mechanism. (Because of the higher power level involved, the 64~ tone was controlled by manually operating a carbon type variable resistor placed as a shunt across the leads to the loud speaker.)

In addition to the necessity of eliminating loudspeaker transients at the onset of the tone, there are two important physiological factors which require that it be built up gradually. First, even though there are no nonharmonic components in the sound waves arriving at the ear, it appears possible that a tone of sudden onset sets up transients in the auditory mechanism resulting in hearing a click. Secondly, H. Davis and others have found that the action currents of the auditory nerve are of greater amplitude for a short period beginning with the onset of a tone. This "equilibration time" is of the order of $\frac{1}{10}$ second. It is desirable to avoid such physiological "on-effects" by raising the level of intensity gradually.

7. *Loudspeaker baffle.* The cage for the animal rests on a table

The baffle on which the loudspeaker is mounted is 8 inches in front of the cage. Due to the thickness of the baffle the animals' ears are approximately 14 inches in front of the leading edge of the loudspeaker cone. The baffle is made of 2-inch fir spiked together so as to form a single rigid piece. On each side is applied 2 inches of Rock-Wool. The baffle is slightly wider than the table, and extends from the level of the table top to the ceiling and against one wall of the room. It is so mounted that it rests on timbers going to the floor, and has no rigid connection with walls, ceiling or table top. The space between the baffle and table is filled with sponge rubber.

8. *Cage.* The bottom of the cage is 2-inch fir planking spiked together into a unit and resting on sponge rubber and Rock-Wool. The animal stands on a sheet metal floor resting on the planking. Three sides and the top of the cage are made of heavy wire mesh. The front of the cage is made of wire screening over 2 inches of Rock-Wool, except for the grille through which the animal works. The grille is 22 inches high and 11 inches wide. It is vertically barred with four $\frac{3}{8}$-inch steel bars. A heavy canvas window shade is mounted below the grille. Ropes lead from it to the experimenter's compartment, so that it can be raised to close the grille. The animal is put into the cage through a sliding door at the side.

9. *Food drawer.* The food drawer and the case in which it slides fit into a cut-out space in the baffle just below the opening for the loudspeaker. The drawer measures 5 inches wide, 4 inches high and 10 inches deep. Its handle is a cylindrical piece of bakelite $1\frac{3}{4}$ inches long and $\frac{7}{8}$ inch in diameter. The handle is wound with a double spiral grille for the administration of shock. The experimenter places the food into the drawer at the rear. Plate I is a photograph of the animal's view of the open grille and food drawer.

10. *Observation of animal.* A mirror is so placed at one side of the baffle that the space between the cage and the baffle is under observation. By this means the hands of the animal are kept in view, but the experimenter is out of sight of the animal. A second mirror, used during the training series, is so arranged

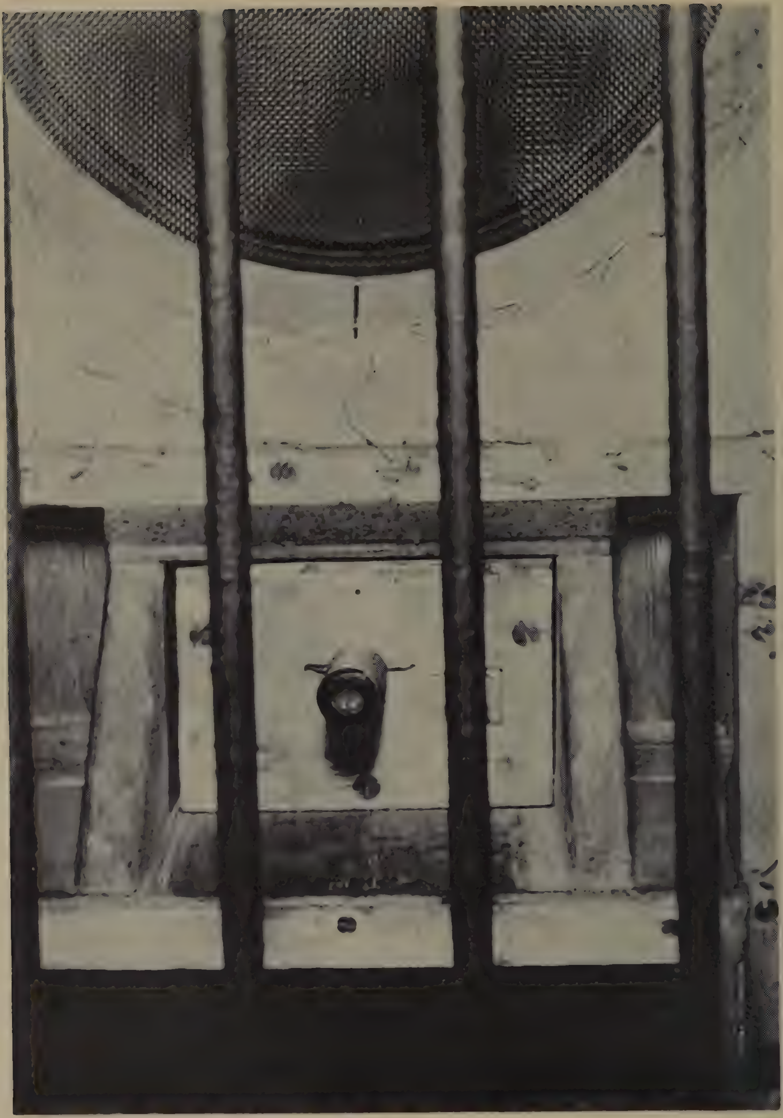


PLATE 1

that it reveals the floor of the cage for a height of two inches, and allows one to observe the animal's position.

11. *Control apparatus.* The apparatus is equipped for remote control of the tone stimuli and for remote recording of stimuli and responses. This equipment was not used in the critical trials here reported, though it was useful during the training and during check experiments.

Discussion of apparatus

a. *Purity of tones.* In auditory limen work it is desirable to secure oscillographic records of the actual sound waves. Such records were not secured. However, it is reasonable to assume that the tones did not contain harmonics which were above the limen of the subjects, except in the case of the 64∼ tone which had audible harmonics when there was 6 db or less of attenuation in the circuit.

The factors affecting tone purity are: 1) harmonic content of the oscillator output, 2) harmonic frequencies set up by partial vibrations and by distortions of movement of the loudspeaker cone (see Knowles (5) for data on the Jensen M20 loudspeaker), 3) the coincidence of harmonic frequencies in the generated sound with resonant frequencies of the enclosed room space, and the reaction of this upon the loudspeaker cone (6), 4) harmonic frequencies arising in the ear and auditory mechanism (3). Factors 2) and 4) are negligible at liminal tone intensities; factor 3) will affect only the low frequencies (up to 512∼?).

b. *Tone intensity.* It should be noted that the intensity control system is probably not perfect. When working at very high values of attenuation (as at 90 db where the ratio of power output of the oscillator to power input to the loudspeaker should be 1,000,000,000:1) the attenuator settings probably do not exactly correspond to the true attenuation values, but, because of current leakage, are slightly larger than the actual amount of attenuation. If this is true, a change from 10 db to 20 db of attenuation represents a greater relative change than from 80 db to 90 db. This would mean that the measured decibels were somewhat smaller than the true decibels, and would reduce the actual amount of the differences between monkeys and man. However, the data contradict this to some extent. If the decibel is smaller at high values of attenuation, the variability of response should increase. This actually does happen, but to only a slight extent; see tables II and V.

c. *Energy value of liminal tones.* It would be desirable so far as possible to determine the intensity of the tones by actual measurement with a calibrated condenser microphone or Rayleigh disk. This has not been done in the present investigation. Instead, the apparatus has been standardized on a uniform group of young human subjects, and then their limens have been assumed to correspond with those reported for a similar group studied by Sivian and White (8) who were able to determine the energy values of their stimuli. The sensitivity of the monkeys has then been evaluated from comparison with the human data. This method is limited in its accuracy by the possibility of a difference in our subjects and those of Sivian and White. The interpretation of the findings should also take into account the difference between humans and monkeys in the obstacle effect of the head to the advancing sound wave. The latter factor is of possible importance at high frequencies, where it may operate to make the humans apparently less sensitive. However, the conditions were such (both monkeys and humans moved the head to "sample" the sound field) that this factor was probably reduced in its effects.

d. *Secondary cues.* There are four possible sources of secondary cues: the experimenter, the control apparatus, vibratory stimuli from the floor or other parts of the apparatus and onset transients in the loudspeaker. The last factor has been discussed above. The control apparatus made no sounds audible to the experimenter, though he was in a far more favorable position to hear them than was the subject. Secondary cues from the experimenter's movements and breathing were controlled by subjecting all of his activities to a rigid routine. The possibility of vibratory stimuli affecting the animal was controlled by a) mechanical isolation of all separate parts of the apparatus, b) very heavy mass of baffle and cage, c) checks for sympathetic vibrations of parts of the cage with tones of the whole frequency range, testing each part by an optical method giving 7,000x magnification and using the full output of the oscillator to produce loud tones. No significant vibrations were found.

The possibility of the operation of secondary cues seems entirely ruled out for the following reasons: 1) The animals readily learn to respond to secondary cues as shown by extensive experience during the preliminary series, and such responses are easily traced to their sources in the apparatus. None was detected in the critical series. 2) Short-circuiting the leads to the loudspeaker or unwittingly leaving the auxiliary attenuator in the circuit results in failure of response, and acts as a check both on the control apparatus and the experimenter. 3) The control apparatus was adapted to a wide range of uses and offered 12 different ways of turning on the tone. Although some of these are completely different from others, variations in the method do not disturb the animal. (For the trials on which limen determinations were made the procedure was rigidly standardized and no such variations were used). 4) The recitation of the above controls is really unnecessary, since the method provides its own controls. As the intensity is reduced, reaction-time lengthens and finally response drops out. If secondary cues were present one could not find a limen. The presence of occasional secondary cues is unlikely in view of the regularity of the psychophysical functions. 5) After finishing the work on 5 human subjects, each was closely questioned about secondary cues. Two of them reported hearing the manually operated resistor used at 64 ~, but did not use the cue. Two of them reported an "on-effect" with the 128 ~ tone, describing it in one case as "coming on with a rush" and in the other "like a gas-burner, when you light it." They denied hearing clicks at the onset of any tones. The on-effect in these cases was probably due to carelessness in getting the level of saline in the control device above the optimum. This should not be called a secondary cue, since it introduces no stimulus other than the tone.

Procedure and training method

1. *General procedure.* The behavior pattern to which an animal was trained required that he come to the grille as soon as the curtain was opened, sit quietly in a listening attitude, and at the onset of the tone (either 8″ or 16″ after the curtain opened) promptly open the drawer and take a piece of food from it. If responses were initiated either before onset or after termination of the tone, the animal received no food. If the animal failed to respond to the tone, it was terminated after 4 seconds.

In half of the trials a tone occurs at eight seconds after the curtain begins to open, in half it occurs at 16 seconds. A predetermined order is used in varying this fore-period: 8″, 16″, 16″, 8″, 16″, 8″, 8″, 16″, 8″, 16″, 16″, etc. The most outstanding characteristic of the method is that there are no trials without tone. By this procedure the animal receives food on every trial unless a false response (response before tone) occurs, or unless the animal fails to react to the tone. Elder has successfully used a method with the chimpanzee in which tones are presented at a constant (5 seconds) interval after exposure of a reaction key, but one-half of the trials are "blanks" with no tone given. The chimpanzee will adapt to this situation, but, with the amount of training given, our monkeys did not. We began with a method modelled from Elder's, and over short periods of time it was sometimes successful. But eventually the animals began to persistently make false responses on each blank trial. The method now used effectively reduces false responses, though even with this method they are rather numerous. We are skeptical of the possibility of entirely eliminating such responses in monkeys when the animals are working on limen determinations.

Monkey No. 2 was subjected to a different method, which will be described in connection with the data on this animal.

2. *Training method.* In all cases the period of training before measurement of limens was protracted, occupying from 81 to 164 sessions, 1203 to 3855 trials (see table IV). This large number of trials is partially accounted for by the fact that the method was being developed with these animals. There was no stand-

ardization of the method of training different individuals, each being treated according to what its individual peculiarities seemed to require. It would not be worthwhile to describe these details. An effective procedure of training is as follows.

Before the first session the animal receives no food for 48 hours. It is then put in the experimental cage. At intervals of one minute the curtain is opened. Ten seconds after opening the curtain a tone (1024 ~ 60 db above the probable limen) is presented and one second later the experimenter pushes out the drawer, having first placed a piece of food in it. The animal will take the food; the drawer is pulled back; the curtain is closed. Some animals will require some preliminary training to take food first from the edge of the drawer, then from the drawer itself. As the animal loses its negative reactions to the apparatus, and takes the food promptly on each trial, the experimenter on succeeding trials pushes the drawer open for a shorter and shorter distance. At some point the animal will begin to pull the drawer open to get the food. When this happens the interval between opening the grille and turning on the tone is shortened to about 3 seconds, and the drawer is held shut by the experimenter until the onset of the tone. The animal will attempt to open it before the tone, but is not allowed to do so. On successive trials the interval between opening the curtain and presenting the tone is slowly increased, until it is being varied between 8″ and 12″. This procedure, with the drawer locked during the "fore-period," is continued until the animal responds promptly each time the tone comes on. During this time the animal will continue to make false responses before the tone. In order to reduce their number a change is introduced. In succeeding sessions the grille is left open during the entire experimental period. The animal is allowed to open the drawer at any time, but receives food only when its response coincides with the tones coming at 1 min. intervals. After this procedure has been used for a considerable time an animal will ordinarily cut down the number of its false responses to one or two per minute, and then it can be initiated to the final procedure. In this the grille is again closed except for the periods during which stimuli occur.

At one minute intervals the grille is opened and the animal given access to the drawer. It may open the drawer, but if this is done before the onset of tone, it receives no food, and does not have another opportunity for 1 minute. If no false response is made, a tone is presented either 8″ or 16″ after the curtain opens. In either case the tone lasts four seconds. If response is initiated during the tone, the animal gets food from the drawer. Under these conditions false responses decrease in frequency in the case of most animals. They are never eliminated. As the response to tone becomes stable, the tone intensity is reduced from day to day. While the animal may respond readily to loud tones, it sometimes requires extensive training to get response to fainter ones, even though these may be 20 to 30 db above the limen determined later.

With the continuation of this procedure the animal should finally begin to take up a position at the grille as soon as it opens, and then assume a listening attitude until the tone comes on. One can now begin to make limen determinations. The first tone of each day is selected to be well above the limen. On each succeeding trial the tone intensity is reduced 2 db until an intensity is reached where the animal fails to respond. At the *first* failure of response the intensity for the succeeding trial is increased 10 db, and then again reduced from trial to trial. Each descending series therefore gives one limen determination. When the limen at one frequency has been determined, a shift is made to the next octave above or below. There usually is a temporary disturbance the first time a new frequency is used.

From now on it is a matter of training the animal until its limens are reduced to the point where they no longer change. This is done by repeatedly finding the limens of the range of tones until there is no further improvement.

3. *Nutrition, experimental food, and method of putting food in drawer.* The animals were fed each day after the experiment. The experimental food was not fed as a part of the regular diet. At the time of the experiments the animals had been without food for the previous 16 to 20 hours. For each individual this was kept as constant as possible, because slight variations often

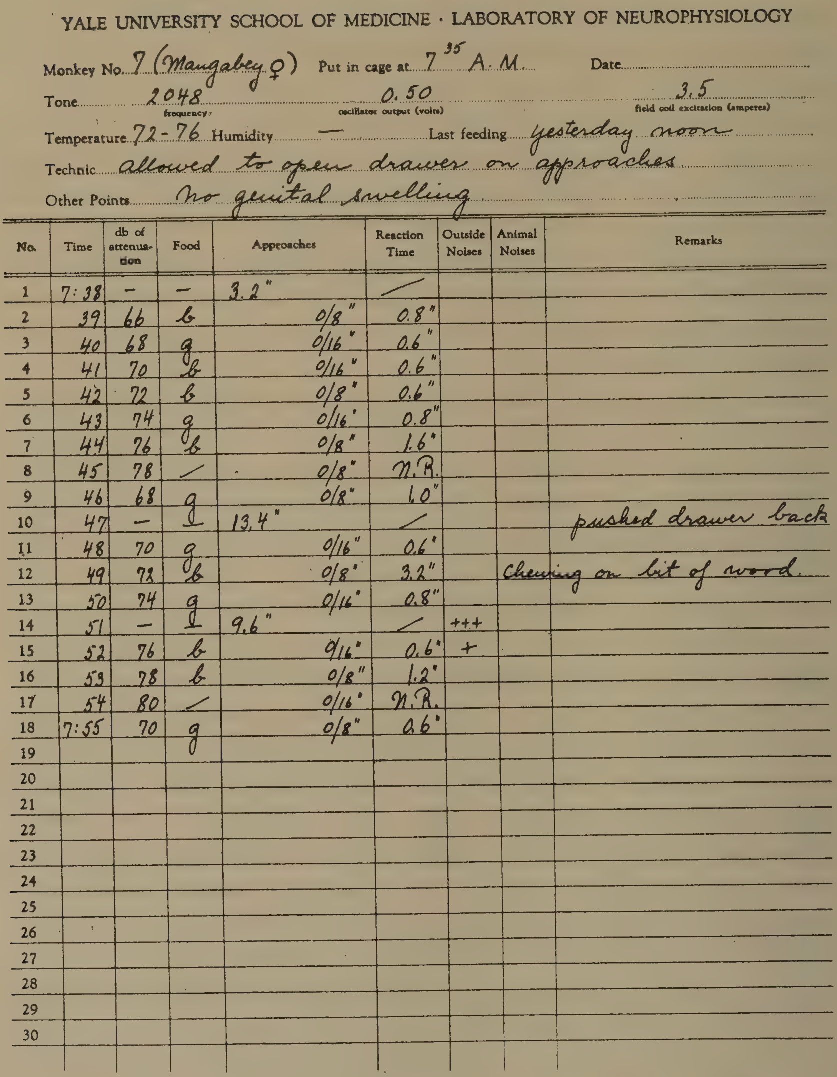
lead to gross disturbances of performance. The animals must be neither too hungry nor too well-fed. The experimental food was banana and grape, and in some cases apple. It was varied in an irregular manner from trial to trial. The food was put into the drawer through the rear, where the end of the drawer was partly cut away. The piece of fruit was speared on the tip of a long knife blade and held over the drawer, but not touching it. If the animal made a false response, the drawer slid out and left the food behind. If the response came during a tone, the point of the knife was lowered *after* the drawer began to move, and contact with the rear end of the drawer dragged off the food and left it in the drawer.

One grape, or approximately $\frac{1}{15}$ of a banana was given at each trial. This amount of food is consumed in 20 to 40 seconds.

4. *Protocols.* Plate II shows a sample protocol. Time between trials, tone intensity, kind of food, length of fore-period or occurrence of false responses and reaction-time to tone were recorded. Disturbing factors and incidental observations were also recorded. A $\frac{1}{10}$ second stop-watch of a satisfactory degree of silence was hung in the path of vision of the experimenter watching the animal. Reaction-times were recorded to the nearest $\frac{1}{5}$ second from the continuously running watch. The errors in this procedure are chiefly constant errors, and probably do not exceed $\frac{1}{5}$ second. Reaction-times were recorded for the period beginning with the onset of tone and ending with the moment the drawer began to move. Since an act of reaching and grasping usually precedes the actual opening of the drawer, the recorded times are all longer than the true times of initiation of response.

5. *Exact procedure.* It is important to specify the exact procedure of such an experiment. The following is an attempt to do this for the critical series where limen determinations were made.

All experiments were done between 6:00 a.m. and noon. The animals were handled by the writer. Each was taken from its living cage and carried or led to the experimental room and placed in the cage. Monkeys No. 1, 3 and 7 were free in the cage, Nos. 2 and 4 were chained to a staple, the former because of resistance to being removed after an experiment, the latter because of a



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Monkey No. 7 (Mangabey ♀) Put in cage at 7^{35} A. M. Date

Tone 2048 (frequency) 0.50 (oscillator output (volts)) 3.5 (field coil excitation (amperes))

Temperature 72-76 Humidity — Last feeding yesterday noon

Technic allowed to open drawer on approaches

Other Points No genital swelling

No.	Time	db of attenuation	Food	Approaches		Reaction Time	Outside Noises	Animal Noises	Remarks
1	7:38	–	–	3.2"		/			
2	39	66	b		0/8"	0.8"			
3	40	68	g		0/16"	0.6"			
4	41	70	b		0/16"	0.6"			
5	42	72	b		0/8"	0.6"			
6	43	74	g		0/16"	0.8"			
7	44	76	b		0/8"	1.6"			
8	45	78	/		0/8"	N.R.			
9	46	68	g		0/8"	1.0"			
10	47	–	g	13.4"		/			pushed drawer back
11	48	70	g		0/16"	0.6"			
12	49	72	b		0/8"	3.2"			Chewing on bit of wood.
13	50	74	g		0/16"	0.8"			
14	51	–	g	9.6"		/	+++		
15	52	76	b		0/16"	0.6"	+		
16	53	78	b		0/8"	1.2"			
17	54	80	/		0/16"	N.R.			
18	7:55	70	g		0/8"	0.6"			
19									
20									
21									
22									
23									
24									
25									
26									
27									
28									
29									
30									

PLATE 2

dangerously vicious disposition which necessitated the chain as a safety measure.

At a vocal signal from the experimenter the animal was given a piece of food. The experimenter then retired to his compartment to record the general data on the protocol sheet and to make instrumental adjustments. The first tone stimulus came 3 minutes after the animal was put in the cage. Its intensity was chosen to be well above the limen. For monkey No. 7 this was usually 12 db above the limen, for Nos. 1 and 4 it was usually 14 db, for Nos. 2 and 3 it was usually 20 db. On each successive trial the intensity was reduced 2 db until a failure to respond occurred; it was then raised 10 db, and again reduced in steps of 2 db on succeeding trials. There were usually two such series each day, though as many as four were occasionally secured. A typical single session therefore contained 15 to 25 trials and yielded 2 limen determinations.

Tones were given at one-minute intervals. Each minute may be divided into four periods: 1) a period of relative silence while waiting until the time for the next trial arrives, 2) a period of preparation for opening the curtain, 3) a period during which the curtain is open and tones are presented, and 4) a period of writing protocols and preparing the apparatus for the next stimulation. Table I shows the actual events of each minute, the times at which they occur, and the range of variation in timing.

Inspection of table I will show that beginning with the experimenter's act of reaching for the curtain cord the animal is stimulated by a carefully timed series of "ready signals." The first warning of the approach of a stimulus precedes the tone by either 13 or 21 seconds. The trained animal begins to come to the grille as soon as the sequence begins, and has therefore been adequately prepared for the occurrence of the stimulus. This method results in considerable uniformity of performance.

If a false response takes place, the drawer is left open for at least 10 seconds.

If the animal fails to respond to a tone within 4 seconds, the noisy closing of a short-circuit switch is the signal that the trial is at an end.

By starting the procedure on each trial at different points on the stop-watch dial, the presentations were so arranged that the actual time between tones was not shorter than 57 seconds and not longer than 63 seconds.

TABLE I

Timing of experimental procedure

TIME	ACTIVITY OF EXPERIMENTER
0.0″– 1.0″ ± 0.2″	Experimenter drags arm along trouser leg and reaches for curtain cord
1.0″– 2.0″ ± 0.2″	Experimenter drags hand along curtain cord and snaps curtain ring off hook
2.0″– 5.0″ ± 0.2″	Period of silence
5.0″– 5.8″ ± 0.2″	Curtain opens
5.8″–10.0″ ± 1.0″	Experimenter (with no attempt to be quiet) takes a comfortable position, places one hand on the tone control switch, and poises the food in the drawer with the other hand
10.0″–25.0″	Experimenter is completely quiet, breathes slowly and shallowly, watches the animal and the stop-watch. During this period the tone is given, either 8 seconds or 16 seconds after the initiation of the act of opening the curtain
13.0″ ± 0.2″ to 17.0″ ± 0.5″	Tone occurs in approximately one-half of the trials
21.0″ ± 0.2″ to 25.0″ ± 0.5″	Tone occurs in approximately one-half of the trials
Remainder of period	(1) Write protocols (2) Adjust attenuator for next trial (3) Cut off tone (4) Close drawer (5) Close curtain (6) Clean off saline switch (7) Reset saline switch (8) Prepare food for next trial (9) Wait until time for next trial

6. *Method of establishing the limen.* In each experimental day there are one or more series of tone stimulations of intensity decreasing in steps of 2 db. The end of each series is always a failure to react. This terminates the series and another is begun. *The lowest intensity in each series to which there is a response is*

taken as the limen for that series. When a number of such series have been secured, the limen values thus determined can be plotted as the psychophysical function. This can then be done at each frequency. Eight measures were averaged at each frequency to establish the average limen.

The presence of false responses is ignored in the calculation of limens. The reasons for this will be discussed (pp. 39–45).

Standardization of the apparatus on a group of human subjects

Inasmuch as there was no provision for measurement of the actual physical intensity of the sound in the region of the animal's head the data are presented in terms of deviations of the monkeys from the average human threshold. Sivian and White (8) have found that the minimum audible intensity in an open sound field varies with frequency. The following values have been estimated from curve 3 of Figure 10 of their paper. These values may be assumed to approximate the limens of our subjects.

Frequency	*db below 1 bar**
64∼	31
128	42
256	57
512	68
1024	76
2048	82
4096	83
8192	76
16384	55

* 1 bar = 1 dyne per sq. cm.

Method

The method with humans was like that used with monkeys, but with the following differences.

The human subject leaned into the cage and faced the loudspeaker at the grille. During the period of listening for the tone he slowly rotated his head through a small arc to sample the sound field. He indicated his hearing of the tone by opening the drawer by means of a piece of rope tied to the drawer handle. Instead of using the preparatory signals as with the animals, a slightly modified procedure was used. A sharp rap with a pencil against the edge of the table was followed after 5 seconds by a jerk at the curtain cord (the grille being open throughout). The tone followed the latter by either 8 or 16 seconds. Silence of the experimenter informed the subject when his response had been to a true tone; the word "wrong" was spoken when a false response occurred.

The data on each subject were taken at a single session of approximately three hours' duration. Between each tone presentation a rest was given, during which the subject could withdraw from the cage. The interval between tones was 40 to 45 seconds. As in the case of the monkeys, the tone intensity was reduced 2 db on each successive trial, and one failure to respond within 4 seconds was taken as indicating that the limen had been passed. After each failure of response a rest was given during which a fan operated in the room. Three times during the experiment a 10-minute rest was given outside the room. These 10-minute rests divided the experiment into 4 periods. The first served as a practice period on the method and for a rough determination of limens. During each of the next 3 periods one limen determination was made at each frequency. Three measures were therefore secured for each subject at each frequency. (The highest frequency, 16384, was used but once, and omitted in the case of one subject.) It may be noted at this time that the three separate determinations averaged approximately the same. The second averaged 0.8 db better than the first, and the third averaged 0.4 db better than the first. (Consult table II for individual data.) Possibly factors of practice and fatigue cancelled one another in these results.

Subjects

Five subjects were used. The group was uniform both in selection and in performance. The subjects met the following requirements:

1. Each was a college student. 2. To his own knowledge each had normal hearing. 3. Each had a history of freedom from ear disease. 4. Each was entirely free from nose, throat or other infections or illnesses at the time of the experiment. 5. Each

had a full night's sleep before coming for the experiment, and each arrived shortly after breakfast. 6. Each had a reputation for coöperativeness and proved himself such in this experiment. 7. Each had previously served from 15 to 30 times as subject in psychological experiments. 8. One was 18 years old, three were 19, one was 20.

Results

The results are given in terms of the amount of attenuation introduced into the circuit between the oscillator and the loudspeaker. These figures are roughly proportional to the level of physical intensity, a high value of attenuation corresponding to a low physical intensity, and *vice versa.* (Even though the response curve of the loudspeaker and the absorptive capacity of the room are known, it is impossible to make any worth-while calculations of physical intensity from them because of unknown factors, such as standing waves, chance coincidence of resonance points with the frequency used, etc.)

TABLE II

Limens of human subjects

FREQUENCY	Bl	Ca	Ch	Da	Me	AVERAGE
64~	8, 8, 6	12, 14, 14	8, 10, 10	18, 18, 22	10, 10, 12	12
128	36, 34, 32	40, 38, 36	36, 38, 38	40, 46, 46	32, 34, 34	37
256	46, 46, 56	56, 56, 56	46, 44, 48	48, 52, 50	48, 48, 48	50
512	68, 68, 70	70, 70, 68	56, 56, 56	64, 68, 66	62, 58, 56	64
1024	68, 76, 76	74, 72, 70	66, 68, 72	64, 66, 64	64, 64, 60	68
2048	72, 74, 76	78, 74, 76	74, 78, 74	74, 78, 74	74, 78, 74	75
4096	84, 82, 82	82, 84, 80	92, 88, 88	92, 90, 86	80, 84, 86	85
8192	28, 28, 28	34, 32, 32	36, 36, 34	40, 40, 48	32, 30, 32	34
16384	—, —, 8	—, —, 24	—, —, 12	—, —, 4	—, —, —	12

Limens of each subject are given in the order of their determination. The figures are in terms of decibels of attenuation introduced into the circuit between the oscillator and the loudspeaker.

In table II appear all of the measures taken on each subject and the average limen of all 5 subjects at each frequency. Had the median been used as a measure of the limen, the figures would have averaged 0.3 db higher; had the best performance of each subject been used as the limen, the values would average 1.8 db higher. The average range of limens taken at the three separate determinations at each frequency was 3.5 db. These facts indicate that the measure of central tendency chosen has very little effect on the conclusions. For making comparisons of man and monkeys, the average has been used.

Other interesting aspects of the data are as follows:

1. *Relation of length of fore-period to performance.* Each subject did better with the 16-second fore-period than with the 8-second fore-period. Slightly over two-thirds of the failures to hear the tone occurred after the 8-second fore-period. Furthermore, the reaction time of each subject was slightly faster with the 16-second period, averaging 0.2″ faster for the group (1.5″ and 1.3″). This difference, however, does not significantly exceed the possible limit of constant errors in reading the stop-watch.

TABLE III

Relation of reaction-time to tone intensity

SUBJECTS	DECIBELS ABOVE THE LIMEN				
	10 db	8 db	6 db	4 db	2 db
Bl	0.9″	1.1″	1.1″	1.4″	1.8″
Ca	1.1″	1.1″	1.3″	1.8″	2.4″
Ch	0.8″	0.6″	0.7″	0.9″	1.7″
Da	1.3″	0.9″	1.2″	1.7″	1.8″
Me	0.6″	0.7″	1.1″	1.0″	1.2″
Average	0.9″	0.9″	1.1″	1.4″	1.8″
No. of responses	26	60	87	114	123

We attribute the poorer performance in the case of the 8-second fore-period to the interference of the process of getting ready to listen.

2. *Relation of reaction-time to tone intensity.* As the intensity of the tone is decreased, the reaction-time tends to lengthen. Table III shows the relation of reaction-time to tone intensity for each subject. Reaction-times are given to the nearest 0.1 second. Figure VIII shows the same facts graphically. The results show

that there is no sharp increase in reaction-time until sound stimuli are close to the limen. The conditions of this experiment differ from those of previous studies (4) of the effect of intensity of stimulus on reaction-time in that our subjects were not instructed to try to attain speed.

3. *False responses.* The five subjects made respectively 6, 3, 3, 14 and 1 false responses. These do not enter into the computation of limens.

II. AUDITORY ACUITY OF MONKEYS

The numbers assigned to the animals represent their position in our experimental series. A total of 11 monkeys have been used, but the limens of only the 5 here reported have been measured.

Monkey No. 1. Female anubis baboon (papio anubis). Estimated age 4 years. She had been in our laboratory 2½ years when the limen determinations were made. She had severe rickets in infancy, and the results of this condition remained. At the time of removal of a temporal lobe just after the limen determinations, some decalcification and thickening of the skull was observed. The etiology of this condition was not determined. Her general health was good. The animal was very friendly and sociable, but excitable.

The preliminary work of developing the apparatus and method was done chiefly on this animal. She had been working for 13 months before the limen measurements here reported were begun, and on two "set-ups" before the final one. Her final adjustment to the experimental situation was quite satisfactory. There were, however, some troublesome factors. In one of the earlier methods of training an attempt was made to eliminate false responses by using an electric shock from the grille on the drawer handle. Though she worked satisfactorily for some time under these conditions, she finally developed interfering reaction-patterns which made it advisable to discontinue the use of shock. (We believe it wholly undesirable to use shock in association with negative stimuli in training experiments with monkeys. It apparently results in far different behavior consequences than the experimenter intends.) In spite of a year of intensive work after this, the old reactions to shock occasionally seemed to intrude as shown by characteristic "testing" of the grille with the finger tips and refusals to touch the drawer handle. When this happened, though she would not touch the handle, she would open the drawer if she could get her fingers behind its edge. This negative reaction to the drawer handle, along with other interfering factors, was probably responsible for a large part of the difference between her performance with the 8-second and the 16-second fore-periods. This animal was also subject to frequent "blow-ups" (Pavlov's "experimental neuroses") which might be manifested either by cessation of responses of drawer opening or by persistent false responses. Sometimes these lapses were associated with slight changes of conditions such as a too thorough scrubbing of the apparatus, a change in the experimenter's clothing or abnormal excitement in the living cage; but in other cases their antecedents were unidentified.

When fully trained her behavior was well-adjusted. During the time the grille was closed the animal climbed to the top of the cage or quietly occupied herself in some other activity. As soon as she heard the experimenter begin to reach for the curtain cord, she started for the grille. After the curtain opened, she sat very quietly with her nose at the bars, often moving her head slightly. When the tone came, she reached out promptly and opened the drawer.

Monkey No. 2. Female macacus rhesus. Estimated age 3½ years. She had been in our laboratory during one year before the limen measurements were made. Her sex cycles apparently began in our laboratory about 6 months before the time of measurement of limens. Her general health was good, though she remained abnormally thin. She was very timorous. This animal had been subjected to a partial temporal lobectomy before training was begun. We have found that unilateral temporal lobectomy has no effect whatever upon auditory acuity, so feel justified in including her data among the normal animals. Her acuity was determined after unilateral temporal lobectomy, and again after partial removal of the remaining temporal lobe. The limens were identical. The data given in this paper are the data taken after the second operation. These are selected because the animal's performance at that time was the most uniform and generally satisfactory.

This animal was used in preliminary experiments on another "set-up." In the final "set-up" she failed to make a satisfactory adjustment to the procedure used with the other animals. An alternative method was therefore used, as follows. The grille was left open throughout the session. The animal had access to the drawer at all times, but the drawer was held shut by the experimenter except when a tone was sounding. At intervals of 50 to 70 seconds a tone was sounded for 5 seconds. If response was initiated within this time, food was obtained. The tone intensity was reduced in steps of 2 db on successive trials. When the animal failed to respond to a tone, the same intensity was again used in the next trial. If she failed to react to two successive tones at a given intensity, we assumed that her limen had been passed. This criterion was an empirical compromise between the frequency of her false reactions and the consistency of her reactions to tone. We do not recommend the method. One could expect it to result in higher limens because of the absence of a ready-signal. The validity of any given reaction as a reaction to tone is hard to evaluate when false responses are frequent. The method places a heavy burden of responsibility on the judgment of the experimenter, since it is possible to influence the results by selection of the time for administration of tones in relation to false responses. It is not feasible to subject the procedure to the rigid rules holding for the other. The method was possible with this animal because she sat quietly during most of the time and because her false reactions were not too frequent. Since our experience with this animal lasted 13 months and covered 235 experimental sessions, we have reason to feel confident that the figures selected to represent her limens are approximately correct. But the quantitative data which tend to prove it will not be presented, since the conclusions do not depend on this animal alone.

The animal spent the time between tones mostly in grooming.

If not especially hungry her position in the cage varied, but she never climbed its sides. If very hungry she tended to stay at the grille. This factor introduced some variability into the results. False responses tended to increase as the time for the next tone came closer.

Monkey No. 3. Female semi-grey spider (ateleus ater). Her age was estimated at 3½ years by Dr. C. R. Carpenter. She was sexually immature. She had been in this country for at least 6 months before we purchased her, and in our laboratory for one year before the limen measurements were made. Her general health was poor and she never ate well. After the limen determination autopsy showed almost complete decalcification of the bones associated with parathyroid hypertrophy. The etiology of this condition has not been determined. The animal was very affectionate.

The limens reported for this animal are the least satisfactory of the group because she never succeeded in maintaining a wholly satisfactory adjustment to the situation for any length of time. The reported measures are probably somewhat higher than the intensities to which she could have responded under better conditions. A more accurate picture of her auditory acuity would perhaps be given by her best performance than by her average performance, for there were exceptional times when her work was satisfactory.

During the period when the curtain was closed, the animal sat in the cage or hung from its side and scratched herself, chattered or whimpered. She did not regularly make use of the signal given by the experimenter when reaching for the curtain cord and often delayed coming to the grille. In such cases a 9- to 12-second fore-period was sometimes substituted for the 8-second fore-period. At the grille she was usually quiet, but often not. She usually rested her hand or foot on the drawer handle, and occasionally her tail. When it was her foot, the reaction-time of responses was increased by the necessity of withdrawing it in order to open the drawer with the hand. She often slapped the handle or made incomplete jerks to open it.

Monkey No. 4. Male black spider (ateleus ater). This was a sexually mature animal whose age was difficult to estimate. In Dr. C. R. Carpenter's opinion the animal may have been as much as 10 years old. He had been in this country for at least 6 months before we purchased him, and in our laboratory for one year before limens were measured. His general health was poor, and he did not eat well. He had a mucous discharge from the nostrils. On some days he appeared definitely ill and was not used in experiments. In general, however, he behaved like an animal in fair health. At autopsy shortly after the measurements were made he was found to have rather severe decalcification of the bones. His temperament was unreliable. At times he was sociable and affectionate; at other times he was vicious and dangerous. In marked contrast with the other animals, he was self-sufficient and the experimenter did not seem to constitute an important part of his environment.

The animal readily adapted to the experimental situation. The limen determinations seemed satisfactory from the behavioral standpoint, but were probably raised, and their variability increased, by the poor health of the subject. During the period when the curtain was closed, the animal characteristically hung from the side of the cage poking at objects or scratching himself. When the experimenter reached for the curtain cord, he started for the grille. There were occasional exceptions to this. While waiting for the tone he sat very quietly (in some cases resting a hand on the drawer handle) and responded promptly when the tone came on.

Monkey No. 7. Female sooty mangabey (cercocebus torquatus atyp.). Her age was estimated at 4 years by Dr. S. Zuckerman. Her sex cycles apparently began 5 months before the limens were measured, and she had been in our laboratory for the two preceding months. Her general health and appetite were excellent, and there was no indication of any physical impairment whatever. She was extremely active and very affectionate, handled by carrying in the arms.

This was our best experimental animal, and her limens are presented in full confidence that they represent her best possible performance under the conditions of the experiment. During the period between trials she was characteristically active: on closure of the curtain she often made a rapid circuit around the cage half-way between top and floor, then either paced restlessly about, chewed at the wooden framework, pulled at the curtain cords, or was active in other ways. In spite of this activity the animal's performance showed the least variability of any subject in the group.

As soon as she heard the experimenter reach for the curtain cord she ordinarily started for the grille. While waiting for the tone, she sat with her nose just at the bars and her hand stretched out toward the drawer. She constantly moved her hand vertically, often touching the drawer handle, and also moving her head vertically. This behavior had the effect of shifting any standing wave patterns, and of sampling the sound field in the region of the ears. Her responses to tone were prompt and clean-cut.

TABLE IV

NUMBER, SPECIES, SEX, AGE	TOTAL NUMBER OF EXPER. SESSIONS	TOTAL TRIALS	SESSIONS TO TRAIN	TRIALS TO TRAIN	CRITICAL* SESSIONS	CRITICAL* TRIALS	RATING OF PERFORMANCE	RATING OF HEALTH	PERIOD OF EXPERIMENTATION
No. 1, baboon, female, 4 yrs.	210	4914	166	3895	28	658	A	Good	Feb. 13, '33 to June 9, '34
No. 2, rhesus, female, 3.5 yrs.	235	3156	95	1617	7	234	B	Good	Mar. 10, '33 to Mar. 21, '34
No. 3, spider, female, 3.5 yrs.	144	2336	105	1398	34	823	C	Poor	Apr. 28, '33 to Apr. 28, '34
No. 4, spider, male, 10 yrs. (?)	119	1968	81	1203	33	638	B+	Poor	Jl. 10, '33 to Apr. 3, '34
No. 7, mangabey, female, 4 yrs.	135	2329	89	1359	29	563	A+	Excellent	Jl. 24, '33 to still living

* By "critical sessions" and "critical trials" are meant those sessions and trials whose data were used to compute the average limen.

Monkeys No. 5, 6, 8, 9, 10 and 11. Another semi-gray spider, another macacus rhesus, two additional sooty mangabeys and two additional baboons have been used. Training has been stopped with four of these because they developed persistent interfering habits. On only one (baboon) was there a limen determination and for him only at 1024∼ where his performance was but 10 db worse than the average of the other animals though his training was brief.

Results

The data on limens are presented and then other aspects of the results which indicate the validity of the obtained limens.

Table IV summarizes some general data on the animals.

As in the case of the human subjects, the raw data secured are the lowest audible intensities expressed in terms of the amount of attenuation introduced into the circuit between the oscillator and the loudspeaker.

Selection of data. The monkeys were trained until limen measurements were possible. Beginning with 8192∼ and going progressively down to 64∼ eight or more consecutive limen determinations were made at each frequency. A shift was then made to 16384∼ where 8 measures were taken. The frequency range was then covered again. If two retests showed a sensitivity shift of 4 db or more, 8 new determinations were made. *To establish the average limens the arithmetic means of the last eight determinations at each frequency were computed.* No data were rejected, except in the case of Monkey 1 where all of the data of two consecutive sessions were rejected because the animal had a "blow-up."

Exception: In the case of monkey No. 2 the last two determinations at each frequency were selected as representative.

Measure of central tendency. Table V gives the average limens of the monkeys as the mean of the 8 limens at each frequency. The median values are 0.15 db higher, on the average, than the means; the best performance averages 4 db higher (monkey No. 1—3.75 db, No. 3—4.8 db, No. 4—5.1 db, and No. 7—2.4 db). It is clear that the trend of the results can be influenced to no important extent by the method of treating the data. (In the case of monkey No. 2 an average of the last two determinations at each frequency was taken as the limen.)

Psychophysical functions. The psychophysical functions of Nos. 1 and 7, 3 and 4 are given in figures III and IV. The horizontal coördinates represent decibels of attenuation; the vertical coördinates represent number of responses at each intensity level. The possible maximum is 8. (It should be borne in mind that the method was such that a single failure to respond was taken to indicate that the limen had been passed. For instance, if an animal responded to consecutive tones of 52 db, 54 db, 56 db, and 58 db of attenuation, but failed with 60 db, the next tone presented was not at 62 db, but at 50 db, and a new series was begun. The limen of such a series was taken to be 58 db. The animals were not given an opportunity to respond to intensities below that at which a failure occurred.) The curves of figures III and IV present all the data used in the computations. From these data are derived the summarized results of table V. In that table are also given the average human limens, as determined with the same apparatus.

TABLE V

Average limens of monkeys

FREQUENCY	MONKEY 1	MONKEY 2	MONKEY 3	MONKEY 4	MONKEY 7	AVERAGE OF 5 MONKEYS	HUMANS
64~	12 ± 2.3	17 (2)	1 ± 2.4	.4 ± 1.6	15 ± 2.4	10	12
128	35 ± 1.7	41 (2)	30 ± 3.2	24 ± 3.8	31 ± 4.4	32	37
256	57 ± 2.1	63 (2)	43 ± 1.9	39 ± 4.7	53 ± 1.7	51	50
512	68 ± 3.0	69 (2)	50 ± 4.2	58 ± 6.8	66 ± 0.9	62	64
1024	66 ± 1.4	69 (6)	63 ± 4.4	66 ± 3.9	74 ± 1.9	68	68
2048	74 ± 2.9	72 (4)	59 ± 5.2	59 ± 4.8	78 ± 0.9	68	75
4096	49 ± 1.7	73 (2)	52 ± 7.0	53 ± 3.3	73 ± 1.9	60	85
8192	54 ± 2.4	54 (4)	41 ± 3.1	42 ± 4.5	47 ± 2.0	48	34
16384	36 ± 3.0	30 (4)	17 ± 2.8	14 ± 2.4	30 ± 1.2	25	12

The average limen of each monkey is expressed in terms of the number of decibels of attenuation introduced into the circuit between the oscillator and the loudspeaker. Variabilities are given in terms of the standard deviations, except in the case of Monkey 2 where the range of the two measures used is given.

Variability of response and shape of the psychophysical functions. In many instances the performance shows a very satisfactory freedom from variability. This is interesting because it shows

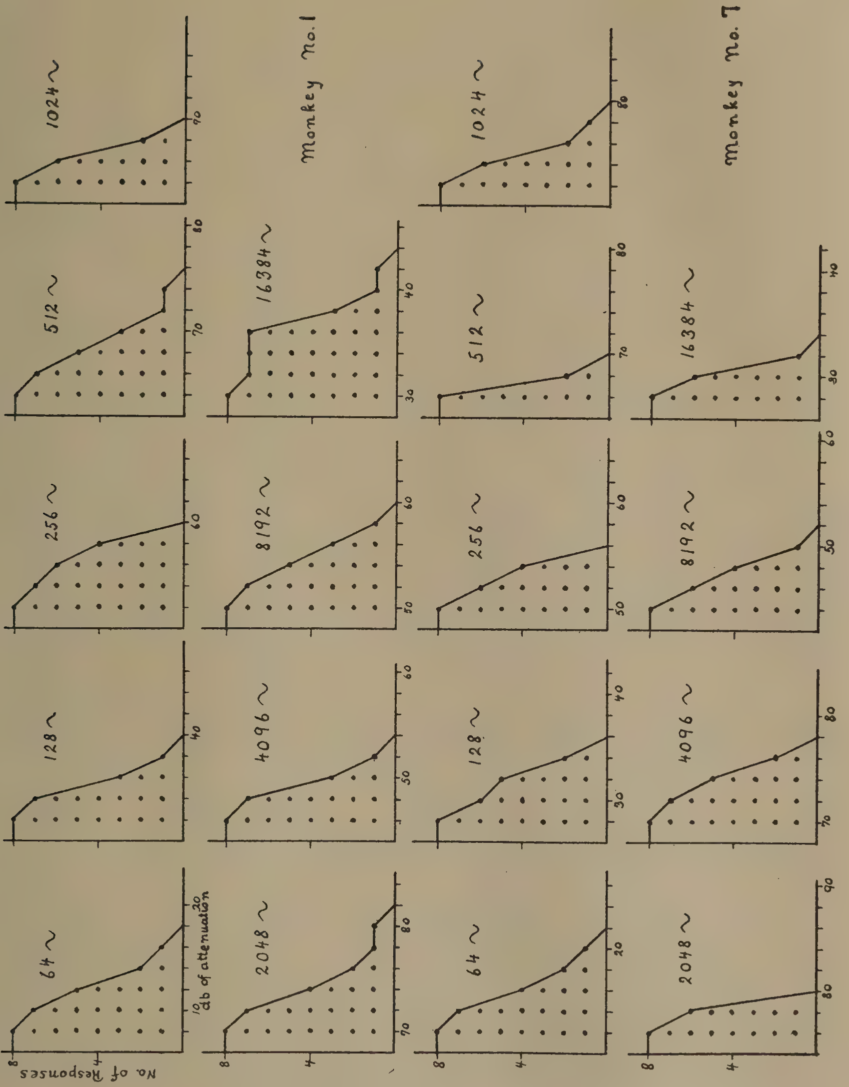
Monkey No. 1
64 ~
128 ~
256 ~
512 ~
1024 ~
2048 ~
4096 ~
8192 ~
16384 ~
Monkey No. 7
64 ~
128 ~
256 ~
512 ~
1024 ~
2048 ~
4096 ~
8192 ~
16384 ~
No. of Responses
db of attenuation
8
4
10
20
30
40
50
60
70
80
90

FIG. III

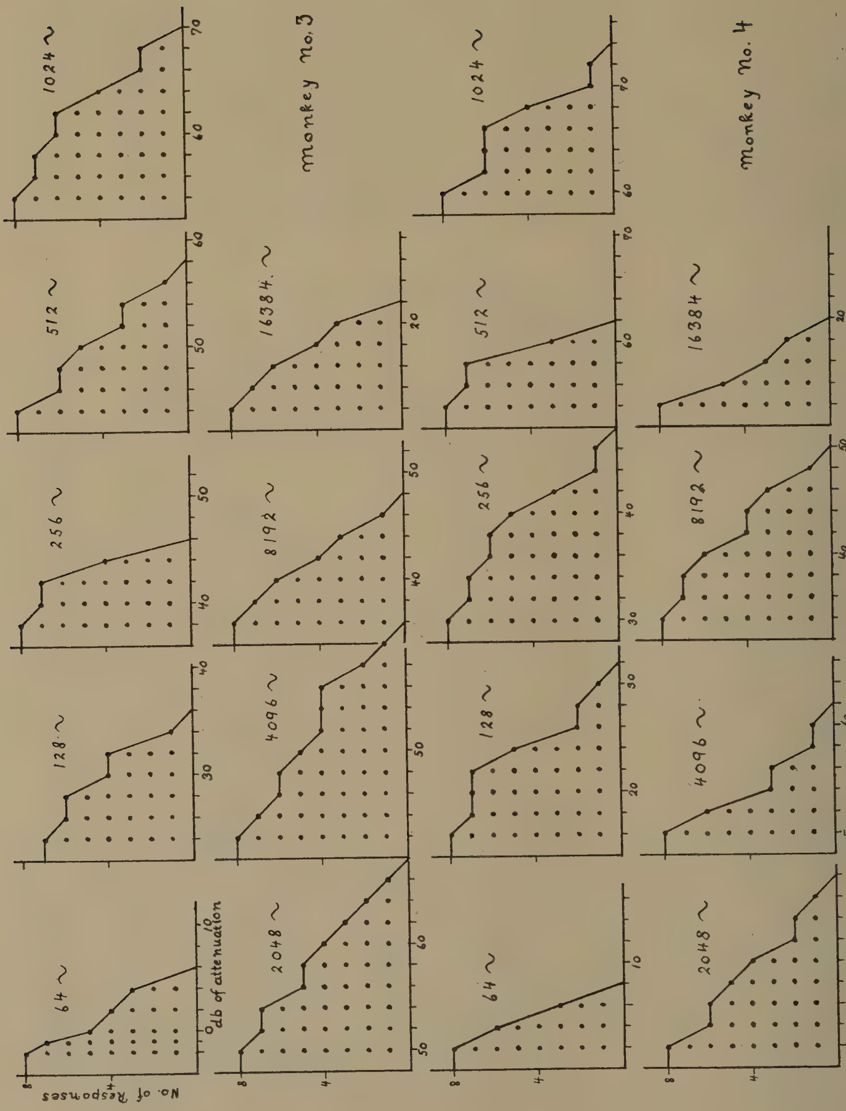
Monkey no. 3
64 ~
128 ~
256 ~
512 ~
1024 ~
2048 ~
4096 ~
8192 ~
16384 ~
Monkey no. 4
64 ~
128 ~
256 ~
512 ~
1024 ~
2048 ~
4096 ~
8192 ~
16384 ~
No. of Responses
db of attenuation
0
4
8
10
20
30
40
50
60
70

FIG. IV

the high level of performance which a thoroughly trained animal can reach, and important because it indicates that the physical conditions of stimulation must have been uniform. The psychophysical functions of monkeys No. 1 and 7, in which the limens are distributed in smooth curves for all frequencies except three, are the best of the group. In the case of No. 7 the limens at 512 and at 2048 had a range of only a single step on our attenuator. This high uniformity of performance is the more remarkable because a single failure of response determines each separate limen, and because the 8 measurements at each frequency are spread over four experimental sessions.

Minimum audible sound field for monkeys. From curve 3 of Figure 10 in the recent publication of Sivian and White (8) the minimum audible sound field for human subjects at the frequencies used in our investigation has been estimated. These are represented in decibels below 1 bar in curve H of figure V. If it is assumed that our human subjects had the same average limens as those quoted by Sivian and White, this curve may be taken as the human audibility curve of this experiment. Curve M of figure V is derived from the deviations of the monkeys from our human group, and may be taken to be the audibility curve of monkeys. Its characteristics will be discussed at a later point in this paper (pp. 45–49).

Such a procedure for estimation of the minimum audible sound field for monkeys is subject to an obvious source of error, i.e., a possible difference between the sensitivity of our group of human subjects and those used to establish the audibility curve given by Sivian and White. A second source of error lies in the probability that the 2 db steps on the attenuator may have been actually slightly less than 2 db, and that the higher the attenuation values, the greater the discrepancy from the true decibel. Such a factor would operate especially for the frequencies from 256 to 4096, and would tend to magnify slightly the obtained difference between monkeys and humans. (See p. 9 above.)

Comparison of monkeys and humans. The results show that the monkeys and humans are very much alike in their sensitivity to tones from 64∼ to 1024∼. At 2048∼ monkeys are slightly inferior to humans. At 4096 ~ they are strikingly inferior. At 8192 and at 16384 the monkeys are somewhat superior. These comparative facts are graphically presented in figure VII in connection with the discussion at the end of this paper.

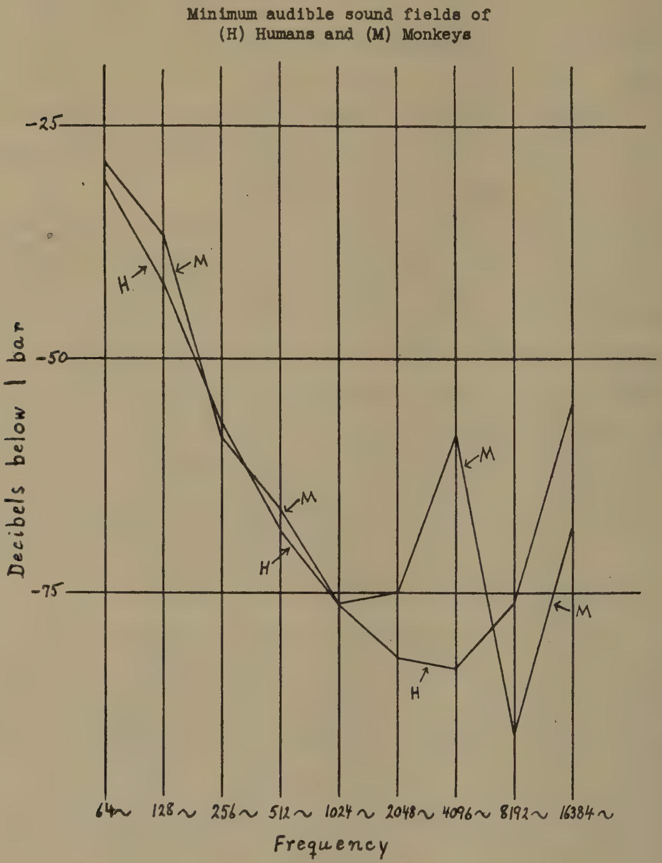

FIG. V

High frequency hearing of monkeys. The hearing of the animals at 8192 and 16384 ~ was superior to that of the human subjects. A part of this difference is attributable to the less favorable position of the human ear on the head. However, we feel that this cannot entirely explain the marked superiority of monkeys No. 1, 2 and 7. There is the added evidence that monkey No. 2 was able to react to tones of 16500, 19000, 20700, 22900, 25000, 30500, and 33600 ~ produced by a Pierce magnetostriction oscillator whose vibrating rod was put in place of the loudspeaker. No higher tones were available for test. This device, and its associated control apparatus for audibility work, was very generously loaned to us by the Laboratory of Comparative Psychobiology, Yale University, from the equipment used by Dr. J. H. Elder. None of the other animals was tested at frequencies higher than 16384.

TABLE VI

Relation of reaction-time to stimulus intensity

SUBJECT	DECIBELS ABOVE THE LIMEN				
	10 db	8 db	6 db	4 db	2 db
No. 1	1.6″	1.6″	1.7″	1.7″	2.3″
No. 2*	—	(2.1″)	(2.5″)	(2.9″)	(2.8″)
No. 3	1.3″	1.4″	1.5″	1.7″	2.0″
No. 4	1.2″	1.3″	1.35″	1.4″	1.6″
No. 7	0.9″	0.9″	1.0″	1.6″	1.6″
Av. of Nos. 1, 3, 4, 7	1.2″	1.3″	1.4″	1.6″	1.9″
No. of responses in av.	157	194	236	259	267

* The data of this animal are not included in the average because they are too few in number to be reliable and because the method used was different.

Effect of unilateral removal of temporal lobe. In the case of monkeys No. 1 and 7 limens have been redetermined after removal of the left temporal lobe. There was no change in sensitivity. These results act as a check on those here reported. These results are in preparation for publication.

Relation of reaction-time to tone intensity. Using all data of all the days whose data were selected for the computation of limens, the relationship between reaction-time and tone intensity has been determined.[2] The average reaction-time at each intensity level appears in table VI. Figure VIII shows the data graphically.

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[2] The trial following a failure to react was not used in the computations because these are affected by a factor having no relation to the present question (see below).

In the computation of these results the intensity deviations from each separate limen determination were used rather than from the average limen.

Table VI shows that reaction-time tends to increase as stimulus intensity decreases. This increase does not become sharp until the intensity is within 4 db of the limen. The trend is true of each animal. The consistency of these results greatly increases the chances of their reliability. Chance errors and constant errors in reading reaction-time cancel one another in these computations. The trend of the results is in complete accord with those obtained on the group of human subjects.

III. DISCUSSION OF DISTURBING FACTORS AND BEHAVIOR DATA

Relation of length of fore-period to performance. As in the case of the human subjects, the performance of the animals was on the whole somewhat better when the fore-period was 16 seconds than when it was 8 seconds. However, with the exception of monkey No. 1, this difference was slight. Failures to respond were slightly more frequent when the tone came at 8 seconds, and 3 of the animals had longer reaction-times at 8 than at 16 seconds. These facts are summarized in table VII.

The differences in the number of failures to respond may be affected by the following factors.

1. A relatively greater number of false responses at 16″ than at 8″ may give an apparent improvement at 16″.

2. At 8″ the animals often have not become completely quiet. Bodily movements, chewing movements, increased respiration from activity, etc. interfere with hearing. They have not yet completely assumed the listening attitude. In some cases they may arrive late at the grille. Such factors were especially important in the case of No. 3.

3. There appears to be a gradually increasing tension during the period of waiting. A less intense tone is then capable of precipitating reaction late in the fore-period. In the case of monkey No. 1 the poorer performance at 8″ was definitely due in large part to the interference of negative reactions to the drawer handle. At a later period of the experiment (after a temporal

lobectomy), when the animal was allowed to open the drawer by grasping its edge, the difference largely disappeared.

4. Opposed to these factors causing poorer performance with the 8″ fore-period was the fact that in some cases the animal stopped "listening" for the tone before 16″ had elapsed, and sometimes even walked away from the grille.

The reaction-time is also affected by these factors. Monkey No. 3 often rested her foot on the drawer handle in the early part of the fore-period, and the shift from foot to hand increased her reaction-times for the 8″ period.

It is not surprising to find such differences in performance. Rather, it is surprising that the differences are not larger. Monkeys No. 3, 4 and 7 have negligible differences in the numbers of failures after the two lengths of fore-period, and monkeys No. 4 and 7 have negligible differences in reaction-time. We estimate that the limens of Nos. 1 and 3 might have been lowered 1 to 3 db, if their performance at 8″ had been equal to that at 16″.

TABLE VII

Effect of length of fore-period on performance

SUBJECT	FAILURES TO REACT		REACTION-TIME	
	Fore-period 8″	Fore-period 16″	Fore-period 8″	Fore-period 16″
No. 1	50	22	1.8″	1.4″
No. 3	40	31	1.65″	1.3″
No. 4	39	33	1.25″	1.3″
No. 7	38	34	1.2″	1.05″
Average	42	30	1.5″	1.3″

Factors influencing failures to respond. Extensive protocols of the behavior of these animals during the training period and during the critical trials were recorded. These reveal many interesting things about the factors which control response. A behavior analysis of this situation is valuable in revealing some of the fundamental processes determining modification of behavior. The writer's experience with these "conditioned responses" of monkeys leads him to a quite different point of view from that of Pavlov and his followers. It is hoped at some time to report this material in full, after our experience with the situation has been increased by experiments now projected.

Some of the factors which are antecedents of failures to respond are extraneous, while others are intrinsic to the situation. Among extraneous factors is the effect of noises originating outside the room. Such noises may act not only to mask the tone, but also operate as distractors interfering with response. However, the presence of noises was ignored in establishing limens. In only a single instance was a tone repeated because of coincidence with a very loud noise on its first presentation. Noise originating from the animal is a second extraneous source of interference. Seven tones were repeated for such causes (animal in motion—2; chewing—2; scratching—2; chattering—1; belching—1). The chief intrinsic factors which affect failures to react are:

1. The first tone stimuli of the day's experiment may not be reacted to unless they are well above the limen. In the critical series 3 tones were repeated for this reason.

2. The first presentation of a new frequency may not be reacted to unless it is well above the limen.

3. If the tone intensity is reduced in steps greater than 2 db, failures of response to tones otherwise above the limen will occur. The animals make an adjustment to the intensity level at which they are working and will not respond if the change is too rapid. In the critical series no steps greater than 2 db were used.

4. Failures to react often follow trials where a false response has occurred.

5. The intrusion of other reaction-patterns often interferes with response to tone: i.e. negative reactions to the drawer, play reactions to objects in the environment, vocalizations, reactions toward the experimenter, and negative reactions to the whole situation arising from repeated failure to secure food by false responses. Reaction to noises, including those from the experimenter, can also be classified here. (Such factors are often described as "inhibitory." As the word is commonly used, "inhibition" describes only the negative aspect of a response picture whose positive aspect is the active responses (see above)

which have gained dominance over the response which one happens to be recording. A more complete and more accurate description of behavior is given by terms which recognize the presence of competing response systems. In order to avoid any misleading implications of a "generalized inhibition," the writer has refrained from the use of the term "inhibition" to describe the behavior of the monkeys in the situations of this experiment (9).)

Many variants of the above factors can be identified. In addition to these specific factors there are such general factors as hunger and general level of performance which influence the number of failures of response and the intensities at which they will occur. Yet in spite of the manifold and variable factors leading to failure of response, some of the animals have a very low variability of response (for No. 7 the average of the SD's is 1.9 db), and the average of all of the SD's for the group is but 3.1 db.

The *total* number of cases where tones were repeated after failure to react was twelve: 1, 2, 6 and 3 respectively for monkeys No. 1, 3, 4 and 7.

The factors which lead to failure to respond in human subjects are comparable to those described for monkeys.

An analysis of false responses. Very frequently the animals did not wait for the tone, but opened the drawer early. Such responses have been called "false responses." The relative frequency of their occurrence varies considerably. Sessions with up to one-third of the total trials terminated by false responses are common. However, a considerable percentage of the days whose data were used were completely free from false response: Monkey No. 1—18 per cent, No. 3—12 per cent, No. 4—30 per cent and No. 7—24 per cent. Furthermore, 15 per cent of the sessions had only 1 to 5 per cent false responses, and 20 per cent had between 6 and 10 per cent false responses. So in over half of the sessions whose data have been used their frequency was so low as to be inconsequential.

The study of the conditions under which false responses occur, and especially of the conditions under which their frequency begins to decrease during training, offers many insights into the behavior mechanisms of the situation. The writer has discussed some of the theoretical implications of these data in a paper presented before the Amer. Psychol. Assoc. on "An interpretation of inhibition of conditioned reflexes as competition between reaction systems" (9). The occurrence of a false response depends on a number of factors. During training these factors change in their strength. For instance, false responses occurring as soon as the grille is opened tend to decrease in relative and absolute frequency as training is continued. The data on false responses included in this paper are taken only from the critical series, although the sessions at an earlier stage of training are in many respects more illuminating on the nature of false responses. Listed below are some of the factors which determine these responses.

1. As the tone intensity decreases, false responses tend to increase.

2. They tend to occur on the trial following a failure to respond.

3. When the tone intensity is suddenly increased on one trial, false responses tend to occur on the succeeding trial.

4. The occurrence of one false response leads to others. Fifty per cent of the total number of false responses occur singly, the remainder occur in groups of two to seven. Within the larger groups there may be two phases: first a phase of decreasing latency where successive false responses come earlier and earlier, second a phase of increasing latency until the tone can be presented at the usual time. We interpret the initial decrease in latency to mean that the failure to secure food acts as a stimulus raising the animal's excitability.

5. When training is incomplete, extraneous noises often excite false responses, as do noises originating from the experimenter. Later this factor becomes of little importance.

6. False responses are likely to follow or accompany other behavior lapses such as refusal to come to the grille, playfulness, etc.

7. Within the situation itself there are a number of factors which are associated with increase in false responses. These factors are inferred from the latency-distribution of the false responses. Table VIII and figure VI summarize the distribution of false responses from the time the curtain begins to open until

the time the tone comes on. The data are taken from only the critical series.

The distribution of these responses in the case of each animal has many points of interest. The table must be consulted for these, but figure VI summarizes the facts. The average values plotted in the figure to some extent give an untrue picture, having their value only because of the fact that the four animals were somewhat similar in their adjustment to the situation. In the case of those individuals whose distribution of false responses differs from the group, the averages are meaningless. The performances of different animals are independent events and the

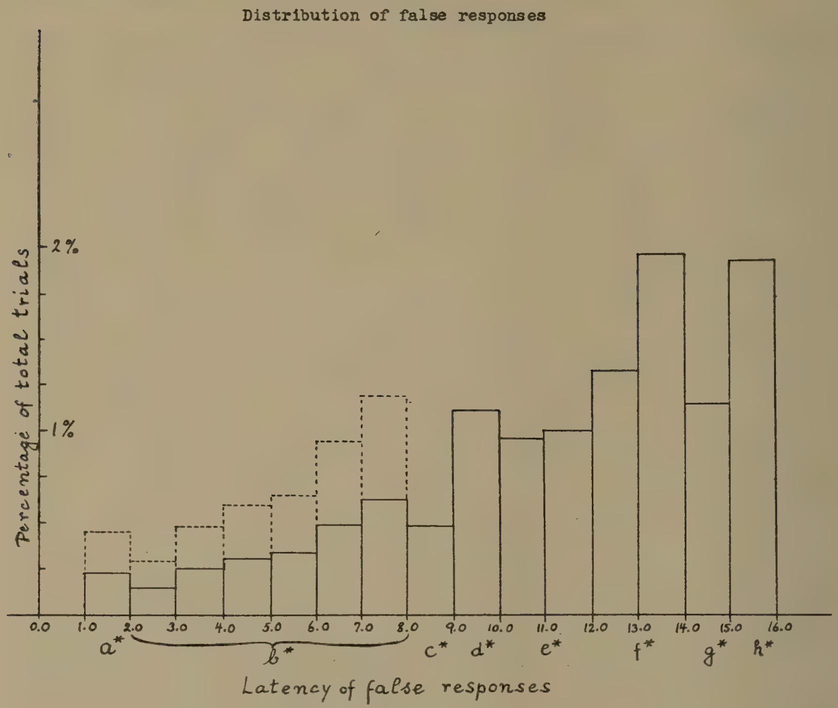
TABLE VIII

Latency of false responses measured from the time the curtain begins to open

LATENCY IN SECONDS	PER CENT OF FALSE RESPONSES IN THE TOTAL NUMBER OF TRIALS					
	Monkey 1	Monkey 3	Monkey 4	Monkey 7	Average	Reduced av.*
0.0″– 1.0″	0%	0%	0%	0%	0%	0%
1.2″– 2.0″	0	0	0	1.8	0.45	0.23
2.2″– 3.0″	0	0	0	1.2	0.30	0.15
3.2″– 4.0″	0	1.2	0	0.7	0.48	0.25
4.2″– 5.0″	0.2	1.1	0	1.1	0.60	0.31
5.2″– 6.0″	0	1.7	0.5	0.4	0.65	0.34
6.2″– 7.0″	0.9	1.0	1.0	0.9	0.95	0.49
7.2″– 8.0″	0.8	1.8	1.7	0.5	1.20	0.62
8.2″– 9.0″	0.6	0.5	0.6	0.2	0.48	
9.2″–10.0″	1.1	1.3	1.6	0.5	1.11	
10.2″–11.0″	0.9	1.1	1.4	0.4	0.95	
11.2″–12.0″	1.2	1.5	0.6	0.7	1.00	
12.2″–13.0″	1.7	1.8	1.1	0.7	1.32	
13.2″–14.0″	2.6	1.7	1.3	2.3	1.96	
14.2″–15.0″	1.1	1.7	1.1	0.7	1.15	
15.2″–16.0″	2.1	1.9	0.6	1.1	1.42	

* The reduced average is the actual average divided by a factor (1.95) which represents the greater number of chances for false responses to occur during the first 8 seconds on account of the use of 8″ and 16″ fore-periods. However, no progressive reduction factor has been applied to take account of the progressively decreasing relative number of opportunities for false response at the longer intervals where a small proportion of the trials has already been used up by false responses.

reliability of an observation on one animal is not to be evaluated by its correspondence or lack of correspondence with others. Inasmuch as no important error of measurement affects the values given, and inasmuch as the time of their occurrence is probably not a function of chance factors, the data of each animal should be evaluated only in the light of that animal. From the table it seems possible to identify 8 periods during the time when the animal has access to the drawer; a) the period immediately following the arrival of the animal at the grille has a relatively high proportion of false responses (true of No. 3 and especially No. 7); b) an increasing number of false responses as the 8″ time for tone is approached (true of Nos. 1, 3, and 4); c) a decrease just



*Explained in text

Fig. VI

at the time when the tone would come on (true of 3, 4, and 7); d) a sharp relative increase immediately after this period (true of all animals); e) a period where there is no further increase (true of all animals); f) a period where there is a sharp increase to a new high peak (true of all animals); g) a period of relative decrease (true of 1, 4 and 7); h) a final increase before the 16″ point (true of 1, 3 and 7). The most interesting period is f), occurring at a time when no stimulus is ever given, yet showing the highest frequency of false response. If we remind ourselves that all of these animals had prolonged training with the situation, we are drawn to the conclusion that many of these false responses can be classed neither as "errors" (i.e. reactions to subjective tones) nor as "anticipatory" responses, but are the result of some factor such as raised excitability from the omission of tone in the preceding period.

8. There are other factors which do not operate consistently, but which can be demonstrated to be active. a) In the trained animal, if one session has many false responses, the succeeding session may be relatively free from them. b) A period of several days when no experiments take place may increase or decrease false responses, depending upon the animal and upon his performance at the time of the break. c) An animal which is too hungry may make more false responses. The same is true of an animal which is not hungry enough. d) False responses may be related to the female ovulation cycle.

Inasmuch as the method of finding the limen ignores the presence of false responses, this procedure requires some arguments to justify it. The data of a session where the frequency of false response was as high as 60 per cent of the total trials of the day have been used. We believe that this procedure is justified, and that it does not affect the results to any important extent. The reasons for this belief are as follows:

1. False responses tend to occur in groups, and their total number is a misleading index of their importance. Seven consecutive false responses have no greater chance of affecting the limen than does an isolated false response. Whereas there was a total of 409 false responses during the critical series, if one counts each

group of consecutive false responses as a single response this reduces to 279. This greatly reduces their importance as an attenuating factor. It would be impossible to calculate their actual contribution to the limens, for reasons which become evident on consideration of the facts discussed above.

2. There is a positive correlation between frequency of false response and excellence of daily limen. The product-moment coefficients of correlation are:

Monkey No. 1	$r = +0.17$
Monkey No. 3	$r = +0.36$
Monkey No. 4	$r = +0.32$
Monkey No. 7	$r = +0.25$

This might be interpreted to mean that the false responses have improved the limen by contaminating the reactions to tone, but a more reasonable explanation is that both limen and false response are affected by increased motivation. If we select those sessions where no false responses occurred and compare their daily limens with the average limens of all days, we find that the performance of Nos. 1, 3 and 4 was worse by respectively 1, 2 and 1 db, and that of No. 7 better by 0.4 db. The small variability of the limens should also be recalled. The average of the SD's for the group was 3.1 db. These facts indicate that any contribution of false responses to the limen must be very slight.

The highest frequency of false response falls in the period between 12.0″ and 14.0″ after the curtain opens, a period where tones never occur. As stated above, it would be incorrect to classify these either as "errors" or as "anticipatory" reactions. A false response of a monkey is probably rarely a reaction to a subjective tone, but is rather the result of an upset of a delicate balance between competing reaction systems: between the listening attitude and the drawer opening response. The slight decrease of false responses between 8.0″ and 9.0″ coincides with the time when the listening attitude would tend to be strongest. Their considerable increase between 12.0″ and 14.0″ probably results from an upset of the balance of rival tendencies by the stimulating effect of the omission of tone in the just preceding period.

A false response is often not equivalent to a true response. If we were to describe the antecedents of these responses in anthropomorphic terms, we would say that they were sometimes reactions of impatience, sometimes of annoyance, sometimes of indifference, sometimes of carelessness, sometimes of uncertainty, sometimes of mischievousness and sometimes of taking a chance. The response pattern may be characteristically different from that of a true response to tone. The animal may open the drawer slowly or in discontinuous steps or only partially, whereas a response to tone is a rapid complete response. He may, on the other hand, jerk open the drawer and leave it without looking for food in it. In some cases the animal's behavior after opening the drawer can be used to infer the antecedents of the response. If an animal opens the drawer during tone, and then does not look at the food placed in it, one may infer that the tone had not been heard and that the response was really a false response. If, after a false response, the animal reaches into the drawer, screams, chatters or pushes the drawer back, we may infer that the antecedents of the response included stimuli to food-taking; but if the animal does not search for food, or walks quietly away, some of the essential antecedents appear to be absent. In individual instances of response such inferences may naturally be in error.

IV. FURTHER DISCUSSION

Comparison of the auditory acuity of man and monkeys. The monkeys had hearing limens equal to those of humans at frequencies from 64 to 1024～; were inferior to humans at 2048 and 4096, with marked inferiority at the latter, and were superior to humans at 8192 and 16384～. These comparative facts have been summarized in figure VII which shows the deviation of the monkeys from the average human thresholds, the average human thresholds being arbitrarily represented as a straight line.

If we compare each monkey to the group of humans on the basis of the average of his deviations from the humans, Nos. 3 and 4 (the spiders) are respectively 9.0 db and 8.7 db worse than humans, and Nos. 1, 2 and 7 are respectively 1.6 db, 5.7 db and

3.3 db better than humans. To some extent the inferiority of the spiders may have been due to their inferior health.

The trend of the data as shown by the average limens for the group of 5 monkeys also gives an accurate picture of the trend

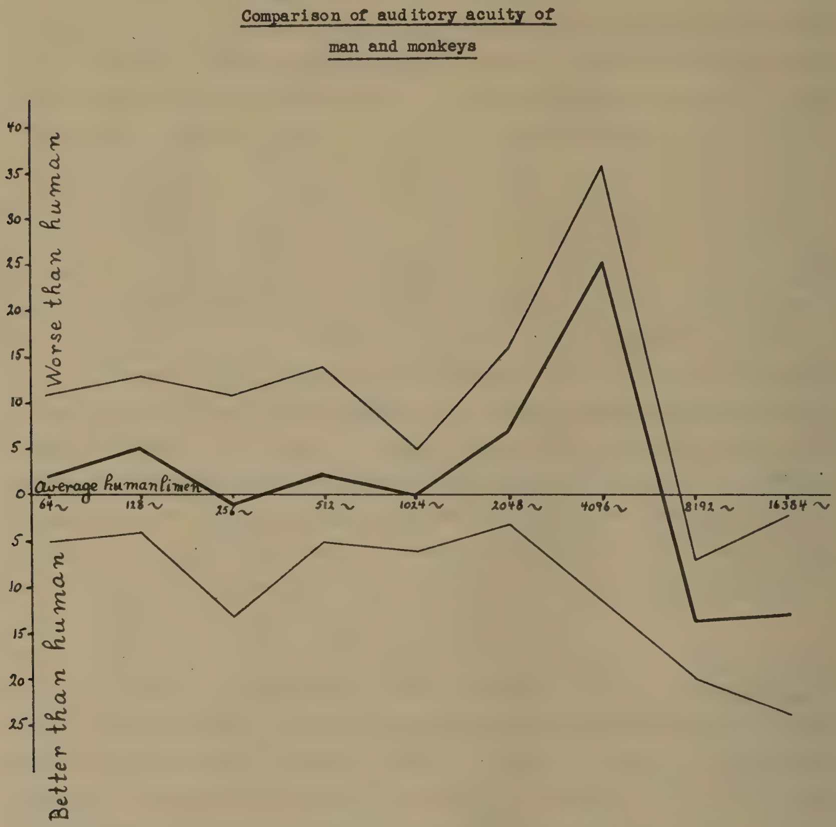


FIG. VII. The average human limens are arbitrarily represented as a straight line. The limens of the monkeys are plotted as deviations from the average human limen. The heavy curve represents the average performance of the group of monkeys. The light curves give the extreme values (i.e. the range) at each frequency.

of the limens of *each* monkey at 2048, 4096, 8192 and 16384. At the lower frequencies, however, there appear to be no consistent trends. These facts appear in table V.

Auditory acuity of chimpanzees and monkeys. Elder (2) has reported the auditory acuity of 3 chimpanzees at frequencies from 128 to 8192. On the whole their performance was about 15 db better than the limens of trained human subjects. The monkeys studied in this investigation appear to be about equal to human subjects when the general level of their performance is taken as a measure of comparison. Elder's chimpanzees were under more favorable conditions than our monkeys, for he was able to keep his animals sitting quietly during the period between tone presentations.

In the general trend of the data there are striking similarities between monkeys and chimpanzees. As in the case of monkeys, the chimpanzees have a sharp drop in auditory acuity at 4096 ∼. At 8192, the acuity of the chimpanzee is more superior to man than at any other frequency tested. These two differences are also the most consistent differences between man and monkeys. In the case of monkeys this trend is even more striking than with the chimpanzees.

The "4096 dip." The hearing curve of monkeys shows a distinct break at 4096 ∼. Any such discontinuity in biological functions should naturally fall under suspicion as a possible experimental error. We have considered this carefully, and can find no factor which can plausibly be called a source of error. The inferiority of the monkeys is too great to be explained away. In the case of monkey No. 1, the limen at 4096 was 36 db worse than the average human threshold, while her performance at the next octave, 8192, was 20 db better than the average human threshold. The animal therefore had a relative shift of 56 db within one octave. The possibility of a change in the instruments between the time the monkey limens and the human limens were measured seems ruled out by the fact that the limens of monkeys No. 1 and 7 were measured just before the work on humans was done and again just after. There was a shift of 1 db in the case of each animal at 4096.

There is, however, one fact which might indicate that the inferences made about the minimum audible intensities expressed in physical units may be in error to some extent. The average

4096 limen of the group of human subjects, expressed in decibels of attenuation introduced into the circuit, was 85 db, while at 2048 it was but 75 db. Measurements of the sound output of M20 loudspeakers have shown their response to be approximately equal at the two frequencies (5). If one were to assume that the attenuation figures are a rough representation of the sound output, one would need to conclude that humans can hear a tone of lesser physical intensity at 4096 than at 2048. However, studies of humans have shown them to be equally sensitive at these two frequencies. This could lead to either of two inferences; 1) that some factor in the apparatus changes the calculations made on the basis of response-curves of the loudspeaker, and that the physical intensity of a 4096 tone attenuated by 85 db is really equal to that of a 2048 tone attenuated by only 75 db; or 2) that our group of human subjects differs from previously reported groups in having better hearing at 4096 than at 2048. We do not have the information which makes it possible to choose between these alternatives. In any event, this factor could explain but a part of the differences found.

The magnitude of the difference between man and monkeys at 4096 ∼ offers the possibility of finding the reason for the so-called "4096 dip." Monkeys should be favorable subjects for anatomical and physiological work aimed at its explanation. The hearing mechanisms of monkeys 1, 3, 4 and 7 have been preserved, but we are not in a position to make anatomical investigations. We will gladly coöperate with anyone who can use this material.

High frequency hearing of monkeys. The auditory acuity of the monkeys was superior to humans at 8192 and at 16384. Monkey No. 2 was also tested with, and reacted to tones up to 33600 ∼, which are definitely out of the human hearing area. This indicates that monkeys are probably superior to humans in upper limit of hearing. We see no reason to doubt this conclusion, though a part of the inferiority of humans may be due to the less favorable position of the ears on the human head.

Low frequency hearing of spider monkeys. At 64 ∼ the liminal tones for monkeys 3 and 4 were associated with harmonics audible to the experimenter. These may have originated either in the loudspeaker or in the internal ear. There is no guarantee that the figures given for the 64~ limen of these two animals are really the limens of that frequency rather than of harmonics.

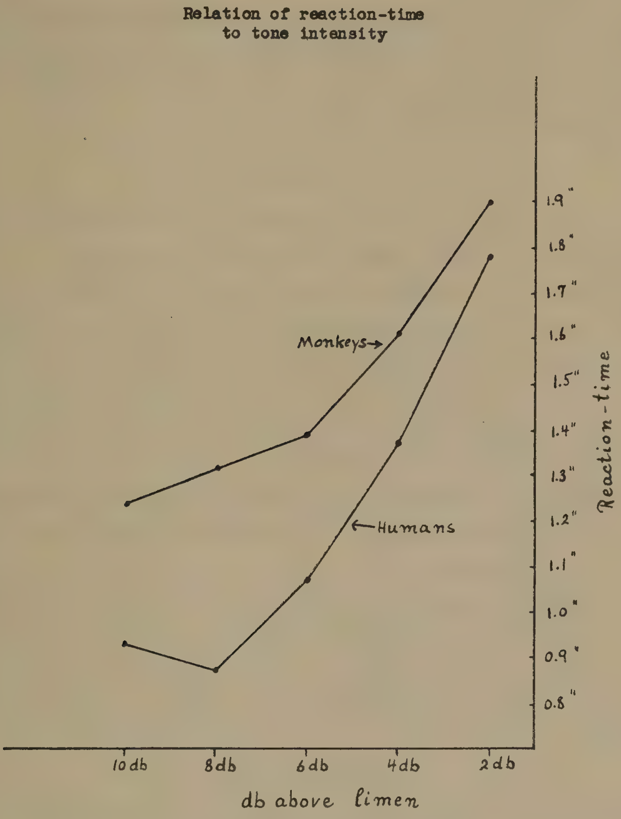


FIG. VIII. These curves are a graphical representation of the data of Tables III and VI. In constructing the curves of reaction-times the 0.01 seconds of the averages were taken into account. (The 10 db point on the human curve is the average of a rather small number of responses.)

However, they stand a good chance of being correct, for the resonance characteristics of the room are such that this tone is about 20 db louder in the experimenter's compartment than at the animal's head, so the harmonics heard by the experimenter may have been inaudible to the animal.

Relation of reaction-time to tone intensity. Kupalov, Lyman and Lukov (7) found the magnitude of conditioned salivary reactions to tone (based on salivation to food) to increase with increase of tone intensity. The present data show that the latency of "conditioned food-taking reactions" is decreased by increase in tone intensity. The interesting feature of the results is that reaction-time does not increase sharply until the tone becomes very faint (within 4 db of the limen). To show this graphically, the data have been plotted in figure VIII.

V. SUMMARY

1. A method and apparatus have been developed for the determination of the auditory acuity of monkeys.

2. The auditory acuity of five monkeys (including 3 species) for pure tones of frequencies from 64 to 16384 was compared to a group of human subjects (average age 19 years). The auditory acuity of the average monkey is equal to that of humans from 64 to 1024~, slightly inferior at 2048, markedly inferior at 4096, and superior at 8192 and 16384~.

3. The relative inferiority of monkeys at 4096 and their superiority at 8192 has recently been reported by Elder to be true also of the chimpanzee.

4. The reaction-time of responses to tone was found to increase with decrease of tone-stimulus intensity. This increase does not become sharp until the tone is within 4 db of the limen.

5. Some behavior mechanisms of the situation have been discussed.

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THE FUNCTIONS OF THE VISUAL AREAS OF THE CEREBRAL CORTEX OF THE RAT IN THE LEARNING AND RETENTION OF THE MAZE. I

BY
YÜ-CHÜAN TSANG
The University of Chicago

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THE FUNCTIONS OF THE VISUAL AREAS OF THE CEREBRAL CORTEX OF THE RAT IN THE LEARNING AND RETENTION OF THE MAZE. I[1]

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[1] The writer is deeply indebted to Professor K. S. Lashley for help and encouragement throughout this experiment and for kindly criticism in the preparation of the manuscript.

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THE PROBLEM

Is the function of the sensory areas of the cerebral cortex strictly sensory or imaginal, or do the areas have some additional function which is not directly related to their sensory processes but is a less specific contribution to the general efficiency of the performance? This question is by no means a new one. Prior to the emphasis on localization in cerebral physiology within the present century, the conception of dynamic functions of the cortical areas played an important part in the theories of cerebral function. Flourens ('42) spoke of an *action commune* in addition to the *action propre* of each part of the brain. In his opinion, it is on account of this fact that the nervous system forms a unitary system. Goltz ('81) also held to a similar view, considering that the capacity for attention represented the psychological aspect of the nonspecific function of the different parts of the cortex. Munk ('81) opposed this with the notion that the interaction of the specialized sensory areas by specific associative connections is sufficient to account for all the functions evident in behavior. With the emphasis on localization the cerebral cortex has come to be regarded as a mosaic of more or less specific functional areas, until recently in the light of the new findings in brain physiology the pendulum is swinging back toward the earlier and more dynamic conceptions.

In the discussion of the peripheral versus cerebral control of the maze performance by Hunter ('30, '31) and Lashley ('31b) the question mentioned above has been raised once more. Hunter does not deny other than sensory functions to the sensory areas; nevertheless, he emphasizes the sensory loss in explaining the relation between the extent of the cortical lesion and the degree of the deficiency of maze performance. He contends that the maze habit involves a sequence of sensori-motor adjustments and that the deterioration in the capacity to learn is brought about by sensory defects, peripheral or cortical, and is in proportion to the number and extent of the sensory areas involved. On the other hand, Lashley points out that the effect of peripheral sense privation on learning is far less severe than that following the destruction of the corresponding cortical sensory projection area and that the more serious effects in the latter case are evidence for the disturbance of some general function other than cortical sensory reception. For him it is chiefly the non-sensory function of the sensory areas that counts more in the efficiency of the maze performance.

The question of the relative effects of peripheral sense privation and corresponding cortical lesion on learning is of great theoretical and methodological importance. A plausible explanation of the relative effects requires a more adequate knowledge of the functions, sensory as well as otherwise, of the sensory areas. There seems to be ample justification for a systematic investigation of the problem of specific versus general functions of the cortical sensory areas, particularly with respect to the visual system. Because it is the most specialized of all the sensory systems, a demonstration of an important non-visual function for it would be suggestive of the same situation in other less specialized sensory fields. The selection of the visual system is further justified by our fuller knowledge of its structure and function and by its easy elimination, peripheral as well as cortical.

To test the functions of the visual cortex we have adopted the following experimental procedure. (*a*) We first determine the character of performance in two similar functions in which vision plays different rôles. This is done by comparing the learning of two mazes of the same pattern, inclosed and open, by normal and by peripherally blinded animals. In the light of the earlier studies of Vincent ('12, '15), Miles ('27), Hunter ('29) and Lashley ('29) we have reason to believe that vision is more important for tracing the open than the inclosed maze. However, we want to test this out in a systematic manner. (*b*) We next determine the influence of the removal of the visual cortex upon the learning of the two mazes. If the function of the visual cortex is exclusively sensory, the consequent retardation in learning should be proportional to the use of vision in the two mazes. In case the effect of the cortical operation exceeds that of the peripheral operation, it would evidently mean that the loss following the operation is more than visual. (*c*) If, as proved to be the case, the cortical destruction should produce a greater retardation of learning than the peripheral blinding, the explanation of this fact might still be one of sensory disturbance. Adult animals may have developed a system of spatial habits in visual terms which would still function in maze learning, even in the absence of vision. Damage to the visual cortex might then disturb maze learning by disrupting the visual space-habits. The alternative to this would be some non-visual function of the visual cortex. To test these alternatives animals are blinded in infancy before the eyes open naturally, thus eliminating the opportunity for building any visual space-habit; and later the effects of injuries to the visual areas are studied.

In the present report we shall confine ourselves to the results reached in the first two steps mentioned above. The results of the third step will form the subject matter of a separate paper.

METHOD AND PROCEDURE

1. Mazes

The inclosed maze is a modification of Lashley's maze III ('29). It measures 147 cm. long and 99 cm. wide, divided into fifteen sections, eight being culs-de-sac. The dotted line in the accompanying figure indicates the correct pathway to the food box. The runway is 6 cm. wide with side-walls 9 cm. high. The starting and food boxes occupy such positions that they do not change the general plan of the maze. Their dimensions are the same as those of a shorter maze section. Both boxes are provided with swing doors controlled by threads. The whole maze is painted dead black. It is raised 51 cm. from the floor and covered with wire mesh. Separate covers of the same material are hinged to starting and food boxes.

The open maze is of approximately the same dimensions as the inclosed, but with no side-walls. The starting and feeding parts of this maze assume the form of a platform. The maze is surrounded by a rectangular screen of black cloth to shut off partially the irrelevant visual distractions.

The visual sensibility of most of the cortically blinded animals was tested on the Lashley jumping apparatus of which several models have been in use in the Chicago laboratory. No description of this apparatus is necessary. The reader is referred to the original literature (Lashley, '30).

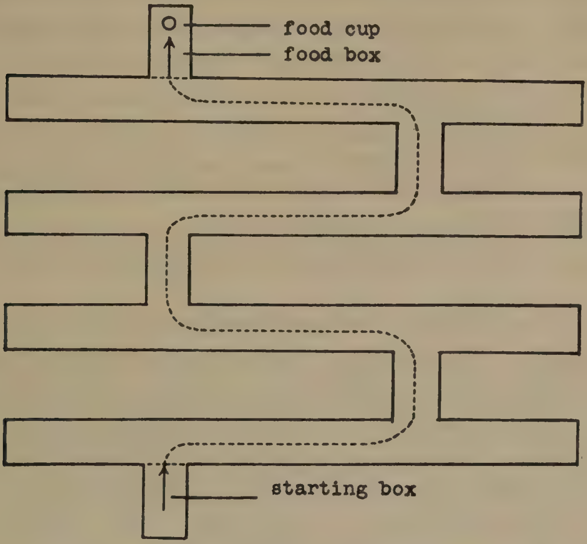

Fig. 1. Ground Plan of the Inclosed Maze

2. Subjects

Ninety-six female rats from the laboratory colony were used in this study. They were hybrids of several strains of *Mus norvegicus* with the hooded blood predominating. Among the animals used Numbers 1 to 36 were albinos extracted from the hooded stock; all the others were hooded. The distribution of these two kinds of rats in the groups was approximately the same. The age ranged from 100 to 150 days at the start of training. Their vision was normal at the beginning of the experiment. The records of several animals were dropped out of account because of ill health, death or infection of the brain.

3. *Training Procedure*

Hunger was used as incentive to learning. The duration of feeding was regulated so that the animals did not take on weight too abruptly. A record of body weight was kept for each animal. The animals were divided into the following groups:

Group I. Normal controls.
Group II. Peripherally blinded: both eyes enucleated.
Group III. Cortically "blinded": visual cortex destroyed, eyes intact.
Group IV. Both peripherally and cortically blinded: both eyes and visual cortex removed.
Group V. A control group, partially cortically blinded: the lesion involving only a part of the area striata, eyes functional.

Each one of the first four groups was again divided into two subgroups, *a* and *b*. Subgroup *a* first ran the inclosed maze, subgroup *b* the open maze. After the learning or failure of the first maze, the animal was transferred to the other maze and trained to the criterion. Two sets of learning records were thus obtained for each maze which served as the first problem for one subgroup and as the second problem for the other. The general effect of blinding on each maze performance was deduced by averaging the scores of the subgroups *a* and *b* for the same problem as a partial control of the transfer effects. Group V was trained in the inclosed maze only.

The regular training took place in the afternoon. The laboratory was artificially and uniformly lighted. Prior to the start of the training in the maze, whether it be the first or the second problem, the animal was fed in the food box or on the platform five minutes daily for three days in succession to get it partially accustomed to the maze situation and to handling, and to associate the maze with food. With the first problem the animal was given a single trial on the first day, two trials on the second day and five trials per day thereafter until the criterion of mastery, ten consecutive errorless trials, was reached or until 150 trials had been given, at which the training was discontinued. For the second problem two trials were given on the first day and five trials per day thereafter. After each successful trial the animal was rewarded with a few bites and then transferred to the starting box or platform for the next run. At the close of the daily training the animal was given its ration in the home cage.

Every effort was made to keep the experimental conditions constant throughout. Olfactory, somesthetic and other sensory factors were not specially controlled. For our problem it makes little difference what sensory cues, other than visual, the animal uses in learning the maze, since we are primarily comparing the effect of peripheral and cortical blinding upon the formation of the habit.

The general procedure for training animals on the jumping apparatus will be given in a later section.

4. Criteria of Learning

The three ordinary criteria of learning, time, errors and trials, have been adopted in the present study. Records were kept for each rat of the total time spent and total errors made in each trial and the total number of trials required to attain the standard of proficiency, that is, ten consecutive errorless trials. On the completion of 150 trials, as mentioned before, training was discontinued and the total number of errorless runs made in the 150 trials was computed. Two types of errors were recorded: (*a*) entrance into blind runways as the animal was moving forward in the direction of the food box or platform; (*b*) retracing over the sections of the true path or into the blind runways while the animal was going toward the starting box or platform.

Of the three criteria the error score is the most reliable. But it should be added that the reliability of the different criteria varies somewhat with the purpose of the study. The gross time score is the most unreliable, because, as Tolman ('21) has pointed out, it is made up of two variables not necessarily related: the "pure speedness," being perhaps a matter of physiological tempo or of temperamental or emotional endowment, and the error-eliminating ability. This is particularly true with the operated animals; here time may mean inactivity. The trial score cannot be evaluated in terms of internal consistency. It may be considerably increased by a few errors and is further distorted in the present study by the arbitrary limit of 150 trials set to the animals. However, it should be noted that our criterion of ten consecutive errorless trials is much higher than ordinarily adopted and the reliability of the trial score is thereby increased considerably. The error score is immune from those sources of error mentioned above and presents the highest consistency. Accordingly, in interpreting our results we shall lay special emphasis on the error scores. The time and trial scores are also presented and give essentially the same results.

5. *Surgical and Neurological Techniques*

All operations were done under deep ether anesthesia with antiseptic technique. The rats in Group II were blinded peripherally by enucleation of the eyes. This could be done rapidly with little or no hemorrhage. Groups III and IV were cortically "blinded" by destruction of the visual cortex. The visual cortex was removed by an electric thermo-cautery through a small trephine hole on the skull in front of the parieto-occipital suture. The eyes of Group IV were enucleated at the same operation. An attempt was made to destroy the visual cortex in its entirety, projection as well as "association" parts. Figure 2 is a reproduction of Fortuyn's ('14) cyto-architectural areas of the rat's cerebrum as modified by Lashley ('29). The strictly visual field, area striata, is largely within the boundary of area w (Herrick, '26, Volkmann, '26, Rose, '29, Lashley, '31). With Group V the lesion was intended for the area striata only. For the operation we used a small scapel instead of the thermo-cautery.

The cortically operated animals were allowed ten days for recovery. At the end of this period training was begun. The allowance for the peripherally blinded animals was three days.

At the completion of training the animal was brought to necropsy. The brain was removed, fixed, cut and stained with iron-hematoxylin. A reconstruction of the cerebral lesion was made on a conventional diagram of rat's cerebrum following Lashley's procedure ('29). For Group V we employed the thionin technique, the sections being much thinner for the convenience of histological examination of the chromatolysis of cells in the lateral geniculate bodies. Rough, off-hand reconstructions were made of the degenerated parts of the last mentioned nuclei as a check on the extent of lesion in the area striata. The total area of cerebral lesion in each case was measured from the diagram with a planimeter and expressed as the percentage of the total surface area of the cerebrum. The area of the non-striate field most involved in addition to the destruction of area striata was also similarly measured and expressed.

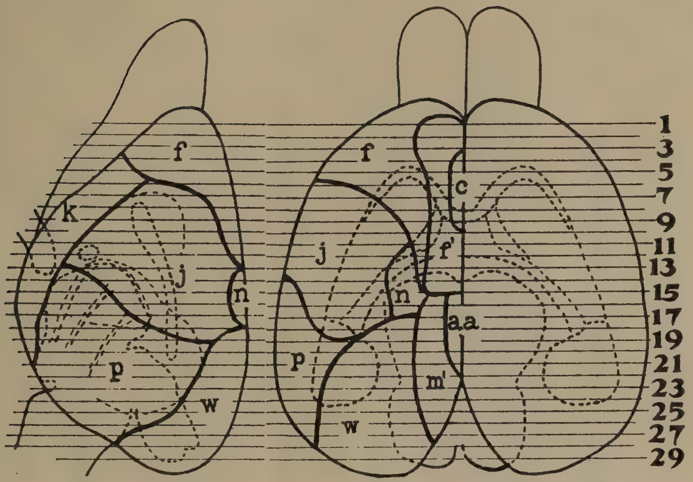

Fig. 2. Fortuyn's Cyto-architectural Areas of the Rat's Cerebrum as Modified by Lashley

The reconstructions of the brain lesions of animals in the various groups are shown in the plates at the end of this report.

RESULTS

1. *Experimental Data*

In Table I are given the individual records of learning of the inclosed and open mazes by the normal animals. Subgroup Ia was first trained in the inclosed and then transferred to the open maze; while Subgroup Ib was first trained in the open and then in the inclosed maze. Total time spent, total errors made and total trials taken preceding the ten consecutive errorless trials are given for each case.

TABLE I

Individual Records of Learning of the Inclosed and the Open Mazes Made by the Normal Controls

Subgroup Ia ran first the inclosed and then the open maze; Subgroup Ib ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials are given for each animal.

ANIMAL GROUP	NUMBER	INCLOSED MAZE			OPEN MAZE		
		Time	Errors	Trials	Time	Errors	Trials
		seconds			*seconds*		
Ia	9	1,988	224	26	383	22	16
	24	3,769	158	97	3,323	163	75
	25	2,033	35	18	313	14	12
	27	3,135	102	32	3,076	83	92
	37	923	56	37	1,485	71	34
	38	276	27	11	272	17	5
	41	8,512	233	61	1,291	57	11
	43	415	28	11	1,236	68	22
	45	2,373	73	31	366	19	16
	46	1,347	92	50	463	26	21
	63	947	59	46	199	17	12
Ib	8	1,521	156	41	472	18	58
	11	354	23	22	2,616	87	47
	26	994	77	46	3,453	101	48
	29	662	37	31	4,083	64	49
	39	1,032	60	68	1,980	99	22
	42	177	10	10	369	15	17
	44	708	43	60	2,375	89	27
	47	2,946	87	24	1,989	52	2
	48	1,014	112	26	525	48	23
	81	377	25	19	5,034	186	58
	94	638	41	69	1,241	65	29

In Table II we present the individual learning scores of the peripherally blinded animals for the inclosed and the open mazes. Subgroup IIa ran first the inclosed and then the open maze; Subgroup IIb ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials, or within 150 trials in case of failure, are given.

TABLE II

Individual Records of Learning of the Inclosed and the Open Mazes Made by the Peripherally Blinded Animals

Subgroup IIa ran first the inclosed and then the open maze; Subgroup IIb ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials, or on the completion of the arbitrary number of one hundred and fifty trials at which training was discontinued, are given for each animal.

ANIMAL GROUP	NUMBER	INCLOSED MAZE			OPEN MAZE		
		Time	Errors	Trials	Time	Errors	Trials
		seconds			*seconds*		
IIa	30	639	54	13	1,902	99	72
	33	8,148	501	101	17,623	651	150 (49)*
	34	296	14	6	1,565	52	56
	35	710	45	23	1,674	98	22
	36	558	53	43	795	60	64
	51	525	28	9	634	33	39
	52	493	35	10	1,028	36	15
	53	836	37	26	7,302	287	150 (60)
	54	4,404	320	86	18,823	614	150 (36)
	61	1,748	62	51	1,379	88	55
	78	2,440	176	93	2,149	148	126
IIb	28	2,356	114	41	25,123	903	150 (26)
	31	542	18	13	2,076	68	62
	32	534	30	17	889	31	28
	40	2,552	181	102	10,747	483	150 (31)
	55	211	16	7	2,190	68	63
	56	141	12	5	572	31	23
	57	4,461	391	132	3,471	441	89
	58	437	26	17	820	46	19
	70	2,171	90	75	7,936	299	150 (56)
	71	652	41	44	11,229	476	150 (46)
	76	1,082	50	34	7,510	241	150 (57)

* Figures in parentheses are errorless trials.

The individual learning scores of the cortically blinded animals for the two mazes are summarized in Table III. The percentage of the total neopallium removed in each case is given. Subgroup

TABLE III

Individual Records of Learning of the Inclosed and the Open Mazes Made by the Cortically Blinded Animals

The percentage of the total neopallium destroyed is given at the left. Brain diagrams illustrating the lesions are given under corresponding numbers in the plates at the end of this report. Subgroup IIIa ran first the inclosed and then the open maze; Subgroup IIIb ran first the open and then the inclosed maze. Group V was trained in the inclosed maze only. Total time, total errors and total trials preceding the ten consecutive errorless trials, or on the completion of the arbitrary number of one hundred and fifty trials at which training was discontinued, are given for each animal.

ANIMAL GROUP	NUMBER	PERCENTAGE OF LESION	INCLOSED MAZE			OPEN MAZE		
			Time	Errors	Trials	Time	Errors	Trials
			seconds			*seconds*		
IIIa	2	21.1	2,387	597	150 (5)	2,798	490	150 (33)
	6	22.1	7,185	885	150 (15)	2,194	267	127
	18	30.4	2,566	379	95	1,702	260	75
	59	14.9	8,430	978	150 (30)	7,791	1,037	107
	62*	22.3	2,054	281	112	713	136	30
	73*	18.3	3,261	472	150 (46)	2,167	256	40
	75*	24.0	3,710	604	150 (17)	1,585	296	119
	77*	32.5	2,605	671	150 (0)	790	106	51
	80*	34.9	3,028	636	150 (25)	2,252	353	115
	82*	27.7	1,931	310	96	947	150	37
IIIb	7	28.5	1,154	93	31	7,641	489	150 (38)
	14	31.5	1,986	374	130	4,073	810	150 (18)
	15	18.7	4,274	769	150 (0)	8,674	1,780	137
	16*	19.2	3,642	535	132	5,029	722	150 (20)
	17	20.0	413	40	14	2,213	247	110
	21*	32.6	1,882	362	63	2,788	501	150 (48)
	68*	14.3	2,231	177	83	2,684	250	138
	79*	31.1	890	201	53	1,281	144	71
	83*	24.0	1,985	166	81	954	166	73
	84*	31.1	890	181	27	1,474	248	85
	87*	31.1	1,029	296	58	852	211	53
V	5	6.0	15,982	386	150 (72)			
	10	6.2	3,610	266	79			
	60	7.2	5,228	677	150 (36)			
	72	6.6	1,559	91	45			
	88	6.2	3,435	270	60			
	97	8.7	30,927	524	150 (63)			
	98	5.7	2,483	380	150 (64)			
	101	7.9	12,705	452	150 (59)			
	102	7.5	3,552	137	150 (86)			
	106	11.3	18,698	595	150 (53)			
	108	7.1	778	49	52			
	109	7.1	3,042	221	150 (74)			
	110	9.2	1,007	81	68			

* Animals whose visual sensitivity has been tested on the jumping apparatus.

IIIa was first trained in the inclosed and then in the open maze; with Subgroup IIIb the order was reversed. Time, error and trial scores are similarly presented for each case. The individual scores and percentages of lesion of Group V, the partially cortically blinded, are also appended to the same table.

TABLE IV

Individual Records of Learning of the Inclosed and the Open Mazes Made by Animals Both Peripherally and Cortically Blinded

The percentage of the total neopallium destroyed is given at the left. Brain diagrams illustrating the lesions are given under corresponding numbers in the plates at the end of this report. Subgroup IVa ran first the inclosed and then the open maze; Subgroup IVb ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials, or on the completion of the arbitrary number of one hundred and fifty trials at which training was discontinued, are given for each animal.

ANIMAL GROUP	NUMBER	PERCENTAGE OF LESION	INCLOSED MAZE			OPEN MAZE		
			Time	Errors	Trials	Time	Errors	Trials
			seconds			*seconds*		
IVa	1	19.1	1,956	261	93	6,637	761	150 (14)
	3	27.9	13,339	2,725	150 (0)	9,313	1,515	150 (6)
	20	35.1	5,036	524	119	2,356	316	150 (45)
	22	35.3	7,792	1,107	107	8,942	843	150 (5)
	23	33.9	3,326	755	150 (10)	8,028	1,142	150 (2)
	50	28.5	1,913	350	128	3,667	600	150 (18)
	64	28.5	2,585	446	150 (52)	2,516	301	121
	85	32.5	2,781	630	131	2,121	407	150 (24)
	90	34.0	11,551	2,343	150 (0)	12,951	1,517	150 (0)
IVb	4	30.2	28,916	1,931	150 (3)	10,878	2,117	150 (0)
	12	33.4	2,288	392	117	4,879	1,122	150 (1)
	13	27.2	1,766	178	107	6,783	897	150 (13)
	65	31.3	1,681	332	117	5,061	886	150 (28)
	66	30.2	3,121	595	116	11,829	1,645	150 (24)
	67	29.2	2,041	274	48	3,756	716	150 (30)
	69	35.8	2,547	419	87	3,309	702	150 (11)
	(74)*	(25.3)	(32,468)	(3,580)	(150) (0)	(17,006)	(1,911)	(150) (0)
	89	21.5	542	54	17	3,807	343	150 (69)

* The unusually poor scores of this animal have been dropped out from group averages.

The individual records of the both peripherally and cortically

TABLE V

Comparison of the Group Average Scores of Normal Controls and of Animals Blinded Peripherally, Cortically and in Both Ways for the Inclosed Maze When This Was Either Their First or Second Problem

The averages are based upon all cases in each group (except Number 74 in IVb) which reached the criterion of learning or completed the arbitrary number of one hundred and fifty trials. The average percentage of cerebral lesions is given for each cortically operated subgroup. Averages of time, errors and trials are given together with their respective probable errors. Under "Difference" the absolute difference between the normal and the operated subgroups is given; under "Percentage" the absolute difference is expressed as percentage of the corresponding average of the normal subgroup; and under "Average Retardation" the average of the three percentage differences is presented.

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESIONS	CRITERIA	AVERAGE SCORES	DIFFERENCE	PERCENTAGE	AVERAGE RETARDATION
			Maze as First Problem				
Ia, Normal	11		Time	2,338.00 ± 449.67			
			Errors	98.82 ± 14.44			
			Trials	38.18 ± 4.86			
IIa, Peripherally Blinded	11		Time	1,891.00 ± 466.46	−447.00	−19.12	
			Errors	120.45 ± 30.01	21.63	21.89	4.18
			Trials	41.91 ± 6.98	3.73	9.77	
IIIa, Cortically Blinded	10	24.8	Time	3,716.00 ± 453.72	1,378.00	58.94	
			Errors	581.30 ± 46.67	482.48	488.24	267.18
			Trials	135.30 ± 4.88	97.12	254.37	
IVa, Peripherally and Cortically Blinded	9	30.5	Time	5,587.00 ± 916.24	3,249.00	138.96	
			Errors	1,015.67 ± 190.89	916.85	927.80	436.53
			Trials	130.89 ± 4.51	92.71	242.82	
V, Partially Cortically Blinded	13	7.44	Time	7,924.00 ±1,635.37	5,586.00	238.92	
			Errors	317.62 ± 36.70	218.80	221.41	221.11
			Trials	115.69 ± 8.23	77.51	203.01	
			Maze as Second Problem				
Ib, Normal	11		Time	948.00 ± 147.95			
			Errors	61.00 ± 8.49			
			Trials	37.82 ± 3.97			

TABLE V—*Concluded*

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESIONS	CRITERIA	AVERAGE SCORES	DIFFERENCE	PERCENTAGE	AVERAGE RETARDATION
			Maze as Second Problem—*Concluded*				
IIb, Peripherally Blinded	11		Time	1,376.00 ± 261.90	428.00	45.15	35.54
			Errors	88.09 ± 21.90	27.09	44.41	
			Trials	44.27 ± 8.10	6.45	17.05	
IIIb, Cortically Blinded	11	25.7	Time	1,852.00 ± 232.05	904.00	95.36	189.65
			Errors	290.36 ± 41.14	229.36	376.00	
			Trials	74.73 ± 8.85	36.91	97.59	
IVb, Peripherally and Cortically Blinded	8	29.9	Time	5,363.00 ±2,128.28	4,415.00	465.72	457.38
			Errors	521.88 ± 131.98	460.88	755.54	
			Trials	94.88 ± 9.58	57.06	150.87	

blinded animals for the two mazes are shown in Table IV. The percentage of the total cortex destroyed is given for each case. Subgroup IVa ran first the inclosed, and then the open maze; the order was reversed with Subgroup IVb. Time, error and trial scores of each animal are similarly presented.

The average scores, time spent, errors and trials made, have been computed for all normal and operated groups for each maze. The records of animals which failed to learn the problem with 150 trials were averaged together with the successful cases of the same group. The group average scores with their probable errors are given in Tables V and VI. Group scores of the four subgroups Ia, IIa, IIIa, and IVa for the inclosed maze, which was run as their first problem, are shown in Table V. The absolute differences in the scores between the normal subgroup and the differently blinded subgroups are presented. The differences are also expressed as the percentages of the corresponding normal scores. The average of the three percentage differences has been computed for each operated subgroup and designated as the average retardation of that subgroup, as compared with the normal

TABLE VI

Comparison of the Group Average Scores of Normal Controls and of Animals Blinded Peripherally, Cortically and in Both Ways for the Open Maze When This Was Either Their First or Second Problem

The averages are based upon all cases in each group (except Number 74 in IVb) which reached the criterion of learning or completed the arbitrary number of one hundred and fifty trials. The average percentage of cerebral lesions is given for each cortically operated subgroup. Averages of time, errors, and trials are given together with their respective probable errors. Under "Difference" the absolute difference between the normal and the operated subgroups is given; under "Percentage" the absolute difference is expressed as percentage of the corresponding average of the normal subgroup; and under "Average Retardation" the average of the three percentage differences is presented.

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESIONS	CRITERIA	AVERAGE SCORES	DIFFERENCE	PERCENTAGE	AVERAGE RETARDATION
Maze as First Problem							
Ib, Normal	11		Time	2,194.00 ± 297.08			
			Errors	74.91 ± 9.14			
			Trials	34.55 ± 3.57			
IIb, Peripherally Blinded	11		Time	6,597.00 ±1,418.64	4,403.00	200.68	215.80
			Errors	280.64 ± 53.55	205.73	274.64	
			Trials	94.00 ± 11.08	59.45	172.07	
IIIb, Cortically Blinded	11	25.7	Time	3,424.00 ± 519.29	1,230.00	56.06	288.39
			Errors	506.18 ± 92.80	431.27	575.72	
			Trials	115.18 ± 7.35	80.63	233.37	
IVb, Peripherally and Cortically Blinded	8	29.9	Time	6,288.00 ± 739.05	4,094.00	186.60	609.03
			Errors	1,053.50 ± 127.25	978.59	1,306.35	
			Trials	150.00 ± 0.00	115.45	334.15	
Maze as Second Problem							
Ia, Normal	11		Time	1,128.00 ± 217.56			
			Errors	50.64 ± 8.76			
			Trials	28.73 ± 5.49			
IIa, Peripherally Blinded	11		Time	4,989.00 ±1,316.48	3,861.00	342.29	271.87
			Errors	196.91 ± 43.93	146.27	288.84	
			Trials	81.73 ± 10.17	53.00	184.48	

TABLE VI—*Concluded*

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESIONS	CRITERIA	AVERAGE SCORES	DIFFERENCE	PERCENTAGE	AVERAGE RETARDATION
Maze as Second Problem—*Concluded*							
IIIa, Cortically Blinded	10	24.8	Time	2,294.00 ± 415.67	1,166.00	103.37	287.10
			Errors	335.10 ± 54.90	284.46	561.73	
			Trials	85.10 ± 8.84	56.37	196.21	
IVa, Peripherally and Cortically Blinded	9	30.5	Time	6,281.00 ± 813.02	5,153.00	456.83	797.27
			Errors	822.44 ± 101.07	771.80	1,524.09	
			Trials	146.78 ± 2.04	118.05	410.89	

scores for the same maze. The average percentages of lesions for the cortically operated subgroups are also appended to the same table.

We have obtained another set of learning records for the inclosed maze with Subgroups Ib, IIb, IIIb and IVb after the completion of their learning of the open maze or after the failure in it with 150 trials. The average percentages of lesions for the cortically operated subgroups are given. Their average records together with the corresponding probable errors, the absolute differences, the percentage differences in the three criteria of learning and the average retardations of the operated subgroups are summarized in Table V.

Similarly, the group average records of the four subgroups Ib, IIb, IIIb and IVb for the open maze, which was their first problem, are presented in Table VI, where the absolute differences, percentage differences and average retardations of the differently blinded subgroups are to be found. The average records of the four subgroups Ia, IIa, IIIa and IVa which ran the open maze as the second problem and the corresponding absolute differences, percentage differences and average retardations of the operated subgroups are also referred to the same table.

The data of those cortically blinded animals which had been tested on the jumping apparatus will be briefly stated in a later section.

2. *The Rôle of Vision in the Two Mazes*

Our results show definitely that the open maze is much easier than the inclosed for the normals as judged by all the three criteria of learning. In the average scores the normal Subgroup Ib, first trained in the open maze (see Table VI), is superior to the normal Subgroup Ia, first trained in the inclosed maze (Table V). With the interchange of mazes this relation is reversed: the same Subgroup Ib when tested in the inclosed maze (Table V) is inferior to Subgroup Ia as tested in the open maze (Table VI). As a concrete illustration we reproduce below their error records for the two mazes:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
Ia (Normal)	Inclosed maze, first	98.82 ± 14.44	
Ib (Normal)	Open maze, first	74.91 ± 9.14	23.91 ± 17.07
Ib (Normal)	Inclosed maze, second	61.00 ± 8.49	
Ia (Normal)	Open maze, second	50.64 ± 8.76	10.36 ± 12.20

We thus see that normal animals invariably made a lower error score in the open than in the inclosed maze, no matter whether the open maze was run as the first or the second problem.

For the peripherally blinded animals the open maze is unquestionably more difficult. This statement is amply justified by the differences between the average records of the peripherally blinded Subgroup IIb in the open maze (Table VI) and the similarly operated Subgroup IIa in the inclosed maze (Table V), and by the complete reversal of the former relations in the records for their second problem (Tables V and VI). We again present their error scores for the mazes in a tabular form at top of page 19. It is plain that the peripherally blinded rats had much greater difficulty in tracing the open maze. They made more than twice as many errors in the open maze as the similarly operated animals in the inclosed.

The relative difficulty of the mazes varies with the presence or

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Inclosed maze, first	120.45 ± 30.01	160.19 ± 61.39
IIb (Peripherally blinded)	Open maze, first	280.64 ± 53.55	
IIb (Peripherally blinded)	Inclosed maze, second	88.09 ± 21.90	108.82 ± 49.09
IIa (Peripherally blinded)	Open maze, second	196.91 ± 43.93	

absence of vision. This suggests the important rôle which vision plays in the open maze. We now compare the learning scores of the normal and peripherally blinded for the same maze. We shall treat the maze problems separately.

a. *Inclosed Maze.* It is clear from Table V that the peripherally blinded rats, Subgroups IIa and IIb, which ran the inclosed maze as the first and second problem respectively were close matches of the normals. The absolute differences in time, error and trial scores are not much greater than the chance deviations of the normal scores. Let us compare their error scores.

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
Ia (Normal)	Inclosed maze, first	98.82 ± 14.44	21.63 ± 33.30
IIa (Peripherally blinded)	Inclosed maze, first	120.45 ± 30.01	
Ib (Normal)	Inclosed maze, second	61.00 ± 8.49	27.09 ± 23.49
IIb (Peripherally blinded)	Inclosed maze, second	88.09 ± 21.90	

The average retardations of these animals are slight when compared with effects of cortical blinding to be presented later, 4.18 per cent for Subgroup IIa and 35.54 per cent for Subgroup IIb. By averaging these two we have arrived at a combined retardation of 19.86 per cent. This probably represents a real difference, but in no case is the difference in maze efficiency between the normals and the peripherally blinded statistically reliable. Furthermore, there is not a single failure among the peripherally blinded in the inclosed maze with 150 trials (Table VII). The effect of peripheral privation of vision on the learning of the inclosed maze is thus not great and of questionable reliability.

b. Open Maze. An entirely different situation exists in the open maze. The peripherally blinded animals are far inferior to the normal controls in maze efficiency (Table VI). We take up particularly the error scores for the open maze of the peripherally blinded Subgroups IIb and IIa which ran this maze as the first and second problem respectively, together with the normal error scores for a comparison:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
Ib (Normal) IIb (Peripherally blinded)	Open maze, first Open maze, first	74.91 ± 9.14 280.64 ± 53.55	205.73 ± 54.32
Ia (Normal) IIa (Peripherally blinded)	Open maze, second Open maze, second	50.64 ± 8.76 196.91 ± 43.93	146.27 ± 44.79

The peripherally blinded animals made about four times as many errors as the normals. Subgroups IIb and IIa show retardations of 215.80 per cent and 271.87 per cent respectively, with a combined retardation of 243.83 per cent. The performance of the animals without eyes in the open maze is more than twice as poor as that of animals with normal eyes. Otherwise expressed, the retardation of the peripherally blinded in the open maze is more than twelve times that of the same kind of animals in the inclosed maze of exactly the same pattern. In contrast to the straight success of the normals, five out of eleven rats in Subgroup IIb or 45.45 per cent and three out of eleven rats in Subgroup IIa or 27.27 per cent failed the open problem, the combined percentage of failures being 36.36 per cent (Table VII).

In short, for the inclosed maze, the effects of the removal of the eyes upon learning are slight and statistically insignificant; whereas for the open maze peripheral blinding has tremendous effects upon the learning scores. The greater rôle of vision in tracing the open maze, as alluded to by previous workers, is thus established beyond any doubt. Thus, in the two similar functions vision plays very different rôles, as expected at the formulation of our research problem. We are now in a position to test the function of the visual cortex in learning the two mazes. If it is purely sensory in function, as said before, cortical blinding should produce the same degree of retardation in the two mazes as does peripheral blinding.

TABLE VII

Number and Percentage of Failures in the Animal Groups for Each Maze

Subgroups a's ran first the inclosed maze; Subgroups b's, the open maze. Group V ran the inclosed maze only.

ANIMAL GROUP	NUMBER OF CASES	INCLOSED MAZE		OPEN MAZE	
		Number of Failures	Percentage of Failures	Number of Failures	Percentage of Failures
Ia, Normal	11	0	0.00	0	0.00
IIa, Peripherally Blinded	11	0	0.00	3	27.27
IIIa, Cortically Blinded	10	7	70.00	1	10.00
IVa, Peripherally and Cortically Blinded	9	4	44.44	8	88.88
Ib, Normal	11	0	0.00	0	0.0
IIb, Peripherally Blinded	11	0	0.00	5	45.45
IIIb, Cortically Blinded	11	1	9.09	4	36.36
IVb, Peripherally and Cortically Blinded	8	1	12.50	8	100.00
V, Partially Cortically Blinded	13	8	61.54		

3. Relative Effects of Peripheral and Cortical Blinding

a. The Character of Vision in Cortically Operated Animals. Before presenting the effects of cortical blinding on maze efficiency we shall state very briefly the condition of visual sensitivity of the cortically operated animals. In the light of the researches of Lashley and his associates we feel sure that animals thus operated still preserve some visual sensitivity. However, we have tested this matter ourselves.

We have trained on the Lashley jumping apparatus six rats of Subgroup IIIa which ran first the inclosed maze and seven rats in Subgroup IIIb which ran first the open maze (cases starred in

Table III). Other animals in these subgroups had already been brought to necropsy when we decided to add this item in our experiment. The animals were trained to jump from a starting platform to a feeding platform against and through one of two cardboard doors on which were glued the stimulus patches. When the animal jumped at the positive stimulus the door was knocked aside and he was rewarded by some bites of food; when the negative stimulus was jumped at he would fall down and get no food. The jumping apparatus was placed against the white wall of the laboratory. The rats learned first to walk, then to jump, through an open door to reach food. After that we put on the white and black cardboards. Ten trials were given daily to each animal. Without any special training, all the animals tested, except two (Numbers 21 and 79 of Subgroup IIIb), jumped directly against the white stimulus card and made twenty errorless jumps consecutively, which was our criterion of mastery for the black-white discrimination.

All these successful animals in the brightness vision test were next subject to the test of horizontal versus vertical stripes. Stripes of glossy white paper, 2 cm. wide, were glued to black cardboard leaving intervals of the same width between them. The horizontal stripes were the positive stimulus. None of the animals passed this test in one hundred trials, at the end of which training was discontinued. The average of errorless trials of the six animals of Subgroup IIIa is 49.50; and that for the seven animals of Subgroup IIIb is 48.57, both being well within the limits of sheer chance. The absence of pattern vision in these animals has thus been proved.

Lashley ('29) suggests the use of pattern vision in the open maze habit. With normal animals the open maze permits more free use of vision for general orientation and for discrimination of the immediate maze pattern. This is chiefly responsible for the more rapid learning of the open maze. Moreover, we found that the cortically blinded animals made fewer errors in the open than in the inclosed maze, when these were their first problems (Tables V and VI). The error score of Subgroup IIIb for the open maze is 506.18, and that of Subgroup IIIa for the inclosed maze is

581.30. Since their visual sensitivity was limited to brightness and position, the natural suggestion is that in the absence of pattern vision this residual visual sensitivity was probably still able to supply visual cues for the general orientation and consequently for the better performance in the open maze.

This relation in the error scores of the same subgroups for the two mazes is reversed when they were run as the second problems. The error score of Subgroup IIIa for the open maze is 335.10 and that of Subgroup IIIb for the inclosed is 290.36. This immediately casts doubt upon the superiority of the open maze subgroup. This problem needs more thorough investigation. Our results do not show decisively just how far pattern vision is or is not essential for the open maze habit. What seems to be true is simply that in the absence of pattern vision the residual position and brightness vision is still capable of providing directive cues for tracing the open maze.

Another fact suggesting the greater use of the residual vision in the open maze comes from the behavior side. Animals with normal and even such partial vision were more or less "seeing" their way to the food platform in the open maze. Their final running seemed to be less automatic than that of similar animals in the inclosed maze, although we are not in a position to furnish quantitative data on the last point.

b. The Inferiority of Cortically Blinded to Peripherally Blinded Animals. (1) Inclosed Maze. Table V presents the average learning records for the inclosed maze of the cortically blinded animals and those of the peripherally blinded for the same problem. The striking inferiority of the former to the latter is convincingly exemplified by the error scores of the cortically blinded Subgroup IIIa which first ran the inclosed maze, and of the peripherally blinded Subgroup IIa for the same maze:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Inclosed maze, first	120.45 ± 30.01	460.85 ± 55.49
IIIa (Cortically blinded)	Inclosed maze, first	581.30 ± 46.67	

The cortically blinded made nearly five times as many errors as the peripherally blinded. Time and trial scores also show similar disproportionate retardations. The average retardation of Subgroup IIIa amounts to 267.18 per cent, being sixty-six times the retardation of Subgroup IIa, 4.18 per cent. Seven out of ten animals or 70 per cent failed to reach the criterion of mastery within the time limit, in contrast to the straight success of the peripherally blinded.

We find the same situation in the records of the cortically blinded Subgroup IIIb which ran the inclosed maze as the second problem (Table V). They were much more retarded than the peripherally blinded Subgroup IIb in the same maze. Let us compare their error scores:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIb (Peripherally blinded)	Inclosed maze, second	88.09 ± 21.90	202.27 ± 46.61
IIIb (Cortically blinded)	Inclosed maze, second	290.36 ± 41.14	

The cortically blinded made more than three times as many errors as the peripherally blinded. The same tendency is obvious in the time and trial scores. The average retardation of the cortically blinded Subgroup IIIb is 189.65 per cent, being five times that of the peripherally blinded Subgroup IIb, which is 35.54 per cent. One failure was recorded in the eleven cases of Subgroup IIIb, or 9.09 per cent, whereas there was none in Subgroup IIb.

The combined retardation of the two cortically blinded Subgroups IIIa and IIIb for the inclosed maze is 228.41 per cent, being eleven times that of the peripherally blinded Subgroups IIa and IIb, 19.86 per cent. Their combined percentage of failures is 39.54 in sharp contrast to the clean record of success of the peripherally blinded.

(2) Open Maze. What has been said of the inclosed maze is generally true of the open maze, though to a lesser degree. Let us select from Table VI the error scores of the cortically blinded Subgroup IIIb and the peripherally blinded Subgroup IIb for the open maze which was their first problem:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIb (Peripherally blinded)	Open maze, first	280.64 ± 53.55	225.54 ± 107.14
IIIb (Cortically blinded)	Open maze, first	506.18 ± 92.80	

The cortically blinded made significantly more errors than the peripherally blinded in the same maze. The former group also took more trials than the latter. The only exception to the general tendency is the time score, to which we cannot give much weight. The average retardation of Subgroup IIIb amounts to 288.39 per cent, being much higher than the 215.80 per cent of Subgroup IIb. Four of the eleven rats of Subgroup IIIb, or 36.36 per cent, failed the open problem; in Subgroup IIb there were five failures among the eleven rats, the percentage being 45.45.

A similar situation exists in the scores of the cortically blinded Subgroup IIIa and the peripherally blinded Subgroup IIa for the open maze when this was their second problem (Table VI). We present their error scores in tabular form below:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Open maze, second	196.91 ± 43.93	138.19 ± 70.31
IIIa (Cortically blinded)	Open maze, second	335.10 ± 54.90	

As compared with the peripherally blinded, animals deprived of visual cortex present a higher error score; their trial score is also higher. Here again the time score stands out as a conspicuous deviation from the general tendency. The cortically blinded show an average retardation of 287.10 per cent, a value fairly constant throughout the cortically blinded subgroups for both mazes. But this value is not much higher than the 271.87 per cent of the peripherally blinded Subgroup IIa for the same problem. One of the ten rats, or 10 per cent, of Subgroup IIIa, and three of the eleven, or 27.27 per cent, of Subgroup IIa, failed the open maze.

The combined retardation of the two cortically blinded Subgroups IIIb and IIIa for the open maze is 287.74 per cent which is still significantly greater than the corresponding 243.83 per cent of the peripherally blinded Subgroups IIb and IIa. However, the combined percentage of failures of the cortically blinded is lower than that of the peripherally blinded, the ratio being 23.18 per cent to 36.36 per cent.

Summing up, from the facts set forth in the present section we see that the cortically blinded animals show a severe retardation in learning the inclosed maze, while the peripherally blinded are not retarded to any significant degree. Undoubtedly vision plays little part in the learning of this maze. We must, therefore, seek the explanation of the tremendous retardation of the cortically blinded in some other source than the defect of vision.

The above statement also holds for the open maze. This is especially true if we lay emphasis on the error scores. The greater retardation of the cortically blinded animals may have been (1) the effects of damage to other sensory areas of the cortex, as contended by Hunter; (2) the effects of disrupting the visual space system which may have been established before the cortical blinding; and finally (3) the effects of the disturbance of non-specific functions of the visual cortex. We shall take up the discussion of this matter in some detail later.

c. Probable Reasons for the Difference in Results between Inclosed and Open Mazes. As we have seen, the contrast between the peripherally and cortically blinded animals is less pronounced for the open maze than for the inclosed maze. This fact calls for explanation. We can only offer our view in a tentative way. After extirpation of the visual projection areas, the diencephalic and mesencephalic visual centers remain functional. Animals thus operated retain unquestionably some brightness and position vision, although the pattern vision is lost (details on preceding pages). This residual vision can be of little help in tracing the inclosed maze due to the "walled-in" condition of the apparatus. On the other hand, the open maze allows greater freedom for such residual vision to function. There is some evidence of its actual functioning in supplying directive cues for running the maze.

Thus, a cortically blinded animal in the open maze can avail itself of a group of helpful cues (e.g. direction of luminous areas in the room) which is not available to a similarly operated animal in the inclosed maze. This might have been the reason for the relatively better performance of the cortically blinded in the open maze and for the lessened contrast in maze efficiency between the cortically and peripherally blinded animals in it.

4. Effects of Combined Peripheral and Cortical Blinding

We had two groups of animals blinded both peripherally and cortically. It was our intention to test whether the removal of the eyes in addition to visual cortex would entail the same effects as the mere removal of the eyes with the brain left intact. We found that the peripheral blinding produced quite different effects under the two conditions. For convenience, we shall take up the effects on the two forms of maze performances separately:

a. Inclosed Maze. Table V gives the average scores of Subgroup IVa, both peripherally and cortically blinded, for the inclosed maze when this was run as the first problem. We tabulate below the error scores of this subgroup together with those of the peripherally blinded Subgroup IIa and the cortically blinded Subgroup IIIa for the same maze:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Inclosed maze, first	120.45 ± 30.01	895.22 ± 193.23
IIIa (Cortically blinded)	Inclosed maze, first	581.30 ± 46.67	434.37 ± 198.79
IVa (Peripherally and Cortically blinded)	Inclosed maze, first	1,015.67 ± 190.89	

Animals blinded both peripherally and cortically made more errors in the inclosed maze than animals operated in either way alone. The time scores are in accord with this general tendency, but the trials scores show some slight inconsistencies. The average retardation of Subgroup IVa runs as high as 436.53 per cent, in contrast to the 4.18 per cent and the 267.18 per cent of Subgroups IIa and IIIa respectively. Four of nine animals, or

44.44 per cent, failed this maze; the corresponding values for Subgroups IIa and IIIa are 0.00 and 70.00 per cent respectively.

Subgroup IVb, blinded in both ways, ran the inclosed maze as the second problem. They were more retarded than animals blinded in only one way. We reproduce the error score of Subgroup IVb together with those of Subgroups IIb and IIIb blinded peripherally and cortically respectively:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIb (Peripherally blinded)	Inclosed maze, second	88.09 ± 21.90	433.79 ± 133.78
IIIb (Cortically blinded)	Inclosed maze, second	290.36 ± 41.14	231.52 ± 139.97
IVb (Peripherally and Cortically blinded)	Inclosed maze, second	521.88 ± 131.98	

Subgroup IVb made more errors in the inclosed maze than either of the other subgroups. They also spent more time and took more trials in this maze than animals operated in either way alone. The average retardation of Subgroup IVb is 457.38 per cent, as against the 35.54 per cent and the 189.65 per cent of Subgroups IIb and IIIb respectively. One of the eight animals, or 12.50 per cent, failed this maze; the corresponding values for Subgroups IIb and IIIb are no higher than 0.00 and 9.09 respectively.

The combined retardation of Subgroups IVa and IVb for the inclosed maze is 446.95 per cent, in contrast to the 19.86 per cent of the peripherally blinded Subgroups IIa and IIb, and the 228.41 per cent of the cortically blinded Subgroups IIIa and IIIb for the same maze. The combined percentage of failures is 28.47, as against the perfect record of the two peripherally blinded subgroups and against the combined percentage of 39.54 of the two cortically blinded subgroups.

We have seen before that the mere loss of eyes has but little effect on the inclosed maze performance, but their loss in addition to the destruction of the visual cortex results in very serious retardation. The effect of peripheral blinding is thus seen to be dependent upon the working condition of the cerebral mechanism.

Moreover, the tremendous deterioration after the combined operation proves the actual functioning of the residual vision in maze running in the cortically blinded animals, though vision is not necessary for it in normals. The visual cues which are dispensable in animals with normal brain become very important for animals whose cerebral mechanism is running at a low efficiency level.

b. Open Maze. A similar situation manifests itself in the records for the open maze of animals blinded in both ways (Table VI). We compare the error scores of Subgroup IVb with combined operation, which first ran the open maze, with those similar records of the peripherally blinded Subgroup IIb and the cortically blinded Subgroup IIIb for the same maze:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIb (Peripherally blinded)	Open maze, first	280.64 ± 53.55	772.86 ± 138.06
IIIb (Cortically blinded)	Open maze, first	506.18 ± 92.80	547.32 ± 166.35
IVb (Peripherally and Cortically blinded)	Open maze, first	1,053.50 ± 127.25	

Animals with combined operation made more errors in the open maze than animals with single operation. The trial scores show the same trend, but some inconsistencies are present in the time scores. The average retardation of Subgroup IVb is 609.03 per cent, in outstanding contrast to the corresponding values of 215.80 per cent for Subgroup IIb and the 288.39 per cent for Subgroup IIIb. The group record is one of straight failures, not a single case of complete learning in the whole group; whereas the percentage failures of Subgroups IIb and IIIb are no higher than 45.45 and 36.36 respectively.

We now turn to the records of Subgroup IVa, blinded in both ways, which ran the open maze as the second problem. They were by far inferior to Subgroups IIa and IIIa, peripherally and cortically blinded respectively. They made more errors than the latter two subgroups as shown on following page:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Open maze, second	196.91 ± 43.93	625.53 ± 110.66
IIIa (Cortically blinded)	Open maze, second	335.10 ± 54.90	487.34 ± 115.02
IVa (Peripherally and Cortically blinded)	Open maze, second	822.44 ± 101.07	

The trials scores are in accord with this general tendency; the time scores are again inconsistent. The average retardation of Subgroup IVa amounts to 797.27 per cent, as against the 271.87 per cent of Subgroup IIa and the 287.10 per cent of the Subgroup IIIa. Indeed, it represents the highest retardation ever suffered by any single subgroup. Eight of the nine animals, or 88.88 per cent, failed the open maze within time limit; while the percentage failures of Subgroups IIa and IIIa are only 27.27 and 10.00 respectively.

The combined retardation for the open maze of the two doubly blinded Subgroups IVb and IVa is 703.15 per cent which is far above the 243.83 per cent of the two peripherally blinded subgroups IIb and IIa and the 287.74 per cent of the two cortically blinded Subgroups IIIb and IIIa. The doubly blinded subgroups show a combined percentage failure of 94.44, while the corresponding percentages of the peripherally blinded subgroups and the cortically blinded subgroups are 36.36 and 23.18 respectively.

Enucleation of the eyes results in tremendous loss of efficiency in the open-maze habit; the same operation in animals deprived of visual cortex produces an extraordinarily serious deterioration. The effect of peripherally blinding is shown once more to vary with the working condition of the cerebral mechanism. That vision is functioning very actively in tracing the open maze in the cortically blinded is also evident from the effect of eliminating their residual vision.

5. *Summary of Experimental Results*

Illustrating more concretely the relative difficulty of the mazes and the relative effects of blinding, single and combined, the combined percentages of failues in the animal groups for the two mazes are represented by the horizontal bars in Figure 3. The length of the bars is proportional to the size of the combined percentages in the various groups. The combined percentages for the inclosed maze is represented by continuous lines; those for the open maze, by broken lines. For the same purpose, the combined retardations of the differently operated animal groups in the two maze habits are similarly diagramed by the horizontal bars in Figure 4. The length of the bars is proportional to the degree of retardation of the animal groups in terms of the percentage of the normal scores for the same problems.

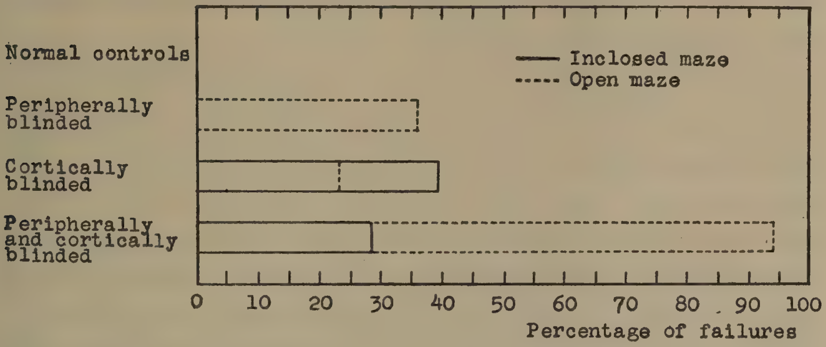

FIG. 3. HISTOGRAM OF THE COMBINED PERCENTAGES OF FAILURES IN THE ANIMAL GROUPS FOR THE TWO MAZE PROBLEMS

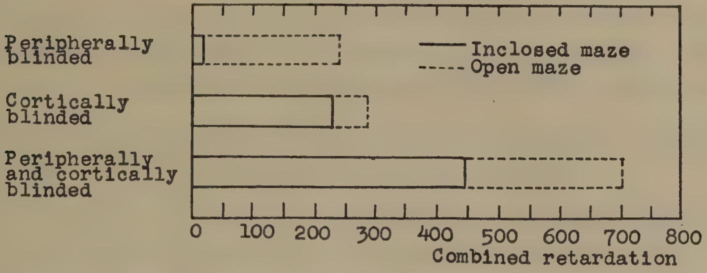

FIG. 4. HISTOGRAM OF THE COMBINED RETARDATIONS OF THE DIFFERENTLY BLINDED ANIMAL GROUPS IN THE TWO MAZE PERFORMANCES

We have given here the scores based upon the average percentage scores of the three criteria, time, errors and trials, in order to take into account the various unknown factors in learning represented by each. Of these the error scores are most reliable and we have stressed them in the preceding discussions. Whether we use the error scores or the combined scores the trend of the results is the same. The trial scores also show the same general trend. The time scores are more often inconsistent, but where they seem to contradict the implications of other criteria, they are generally statistically unreliable.

Let us sum up the main points of our experimental results in a few lines. Animals with normal vision invariably make better records in the open than in the inclosed maze. On the other hand, animals deprived of the eyes are at a conspicuous disadvantage in the open maze. The open maze habit normally involves vision to a great extent. Cortical blinding is generally more disturbing for maze learning than extirpation of the eyes. The contrast is more pronounced in the inclosed than in the open maze where the residual vision after cortical operation plays a larger part. The combination of peripheral and cortical blinding produces more severe retardation than either one alone.

Since the cortical operations involved somewhat more than the area striata, we must consider the effects of this additional destruction before attempting to interpret the data.

6. Possible Influences of Additional Subcortical and Non-striate Cortical Lesions on Learning Scores

The first question to be settled in relation to our data concerns the possible effects of lesions involving non-visual areas of the cortex. Hunter ('30) has interpreted Lashley's data on the correlation between extent of lesion and retardation as due to the involvement of more than one sensory field in the larger lesions. It is absolutely necessary to control our results as to the possible influences of additional non-striate cortical and subcortical injuries.

a. Anatomical Topographical Relations of the Non-striate Cortical Areas Frequently Involved in the Operations. Recent work indicates that the extent of the area striata is somewhat less than that implied in Fortuyn's diagram (Volkmann, '26; Lashley, '34b).

Anteriorly it begins at about level 19 of Fig. 2 and extends to the caudal pole of the hemisphere. The medial border corresponds pretty closely with the edge of field w, but the area is only two thirds the width shown in the diagram, so the lateral border should lie farther to the right.

The adjacent sensory projection areas are probably those of audition, olfaction and general sensation. Lesions in the lower part of field p are followed by retrograde degeneration in the medial geniculate body, indicating in conformity with Wiley's experiments ('32) that this region has auditory functions. Between this field and the area striata there is a zone, at least as broad as the latter, injury to which results in no thalamic degeneration. In front of the area striata is a zone, extending from about levels 9 to 14, lesion to which is followed by degeneration of the lateral thalamic nucleus. Between it and the area striata there is also an area of non-sensory cortex. Mediad to the area striata, the cortex, i.e., the supposed visual association areas, m′, and aa, is in close association with the hippocampal structures and is probably olfactory in function. The studies of Swann ('34) show that olfactory discrimination is not disturbed by destruction of this zone or of the dorsal convexity of the hippocampus. It is thus evident that lesions which exceed the limits of the area striata by a considerable extent (2 mm. or more) do not invade any other cortical fields which are primarily sensory. Lashley and Frank ('34c) have shown that destruction of any region adjacent to the striate cortex and of any part of this field itself do not seriously disturb retention of habits based on pattern vision, so long as some part of the binocular projection field remains intact. Such results indicate that trophic disturbances sufficient to interfere with the function of sensory fields are not usually produced by lesions adjacent to the fields.

We have attempted to destroy completely the visual parts of the cortex, projection as well as "association" areas, that is, fields w and m′ and aa. When our work was begun, fields m′ and aa were still regarded as visual associational and were thereupon destroyed intentionally. This explains the rather constant involvement of these areas in the inflicted lesions. For convenience, we still call them visual associational in the following discussions. The cortical field next most involved is area p, owing to its topographical contiguity to area w and to the difficulty of controlling the depth which the thermo-cautery goes in destroying the latero-caudal part of area w. The caudal points of fields f, f′ and n (motor), antero-medial to area w, and the dorso-caudal wedge of field j (somesthetic), antero-lateral to area w, are also frequently involved, but the injuries rarely amount to any important proportions.

The thermo-cautery is not a satisfactory instrument for inflicting injury to a limited spot; a greater or less involvement of the dorsal convexity of hippocampus is hard to avoid, as the visual cortex is the thinnest part of the whole neo-pallium. In some cases with extensive injuries the lateral geniculate body, the anterior nucleus of thalamus, or the superior colliculus (in very few cases, also the inferior colliculus) of the midbrain is involved. These non-visual parts of the cortex and the subcortical tissues might have something to do with maze performance. We shall try to control the effects of the strictly visual striate lesions in comparison with the possible influences of subcortical injuries and of various non-striate cortical lesions taken as a whole and separately.

b. Possible Influences of Subcortical Injuries. Table VIII presents a comparison of the error scores of animals with and without additional subcortical lesions for the inclosed and open mazes which were run as their first problems. The reason for the selection of the error scores for separate treatment is their generally acknowledged high consistency and reliability as an index of maze efficiency, as discussed in a former section. The conditions of the learning of the first maze are also unquestionably simpler as compared with those of the second problem. From Table VIII we see that the differences between the cases with and without subcortical lesions are not constant. Where the former make poorer scores in the inclosed maze the differences are insignificant in comparison with the inferiority of both groups to the peripherally blinded animals (see Table V). Moreover, the cortical lesions in the animals with subcortical injuries are greater than in the others

TABLE VIII

Comparison of the Error Scores of Animals with and without Subcortical Lesions in Addition to the Destruction of the Visual Cortex for the Inclosed and Open Mazes Which Were Their First Problems

Subgroups IIIa and IIIb were cortically blinded; subgroups IVa and IVb were both peripherally and cortically blinded. Under "effect" the apparently positive (+) or negative (−) influence of the additional subcortical lesions upon the error score is presented.

ANIMAL GROUP	KIND OF LESION	WITH SUBCORTICAL LESION				WITHOUT SUBCORTICAL LESION			EFFECT
		Cases (Experimental Number)	Number of Cases	Average Percentage Lesion	Average Error Score	Number of Cases	Average Percentage Lesion	Average Error Score	
		Inclosed Maze							
IIIa	Thalamic	75, 80	2	29.5	620.00	8	23.5	571.63	+
	Mesencephalic	73, 75, 77, 80, 82	5	27.5	538.60	5	22.2	624.00	−
	Hippocampal:								
	Light	6, 18, 59, 62, 77, 82	6	25.0	584.00	2 (Nos. 2, 73)	19.7	534.50	+
	Extensive	75, 80	2	29.5	620.00				
IVa	Thalamic	22, 23, 90	3	34.4	1,401.66	6	28.6	822.67	+
	Mesencephalic	1, 90	2	26.6	1,302.00	7	34.2	933.86	+
	Hippocampal:								
	Light	3, 50, 64, 85	4	29.4	1,037.75	1 (No. 1)	19.1	261.00	+
	Extensive	20, 22, 23, 90	4	34.6	1,182.25				
		Open Maze							
IIIb	Thalamic	14, 87	2	31.3	510.50	9	24.4	505.22	+
	Mesencephalic	17, 68, 84	3	21.8	248.33	8	27.1	602.88	−
	Hippocampal:								
	Light	14, 17, 68, 79, 83, 84	6	25.3	310.83	3 (Nos. 7, 15, 16)	22.1	997.00	−
	Extensive	21, 87	2	31.9	356.00				
IVb	Thalamic	12, 65, 67	3	31.3	908.00	5	29.0	1,140.80	−
	Mesencephalic	65, 66, 67	3	30.2	1,082.33	5	29.6	1,036.20	+
	Hippocampal:								
	Light	4, 13, 66, 69	4	30.9	1,340.25	1 (No. 89)	21.5	343.00	+
	Extensive	12, 65, 67	3	31.3	908.00				

(Table VIII) and this fact alone is sufficient to account for the greater retardation.

Lashley ('29, '33b) has attempted to estimate the possible influences of the subcortical lesions on the maze learning in various ways. He has never found that the inclusion of cases with thalamic or hippocampal lesions in the whole series alters significantly the results from those which would have been obtained if only cases with neo-palliate lesions were included in the computation of the constants. This is in general true of our results. We may substitute the average error score of the cases within a subgroup either with or without such subcortical lesions for the error score of the whole subgroup without altering the rank of this subgroup among the normal and operated subgroups for the same problem. For instance, taking the cortically blinded Subgroup IIIa in the inclosed maze (Table VIII), there have been computed six error scores (the two scores for the hippocampal cases are averaged together) for the three different groupings with and without a certain kind of subcortical lesion: viz., 620.00 vs. 571.63; 538.60 vs. 624.00; 602.00 vs. 534.50. Any one of these scores may be substituted for the score of the whole subgroup 581.30 without affecting the rank of Subgroup IIIa as intermediate between the peripherally blinded Subgroup IIa and the peripherally and cortically blinded Subgroup IVa in the matter of errors in learning the same maze. The same is true of the error scores of other animal groups for the maze problems. Exceptions are the error scores of the two cases without any hippocampal injury in Subgroups IVa and IVb for the inclosed and open mazes respectively. Since there is only one animal in each case, no importance should be given. The additional subcortical lesions do not seem to influence the group error scores in any specific way.

c. Possible Influences of Non-Striate Lesions Taken as a Whole. In an attempt to destroy completely the visual cortex, the visual association areas m′ and aa, the dorsal edge of the auditory area, p, the dorso-caudal part of the somesthetic area j, the caudal parts of the motor areas f, f′, and n, were rather frequently involved in the cortically operated animals. This is especially true of the supposed visual association areas which were destroyed intentionally. It is practically not feasible to separate the cases with from those without extra-striate injuries in the regular animal groups and determine the possible effects of these injuries upon the learning scores. However, we can determine the possible influences of extra-striate lesions by comparing the scores for the inclosed maze of Subgroup IIIa and Group V. The former was with such extra-striate lesions, while the latter was practically not (details in a later section). Subgroup IIIa made naturally more errors than Group V, the ratio being 581.30 to 317.62. The group average retardations are 267.18 and 221.11 respectively. Though cortically blinded only partially, Group V was by far inferior to the peripherally blinded Subgroup IIa for the same problem. The latter made an error score of 120.45, with an average retardation of 4.18. The control Group V may well be substituted for the regular Subgroup IIIa without altering the rank of the cortically blinded animals as intermediate between the peripherally blinded Subgroup IIa and the both peripherally and cortically blinded Subgroup IVa. The additional involvement of the extra-striate fields taken as a whole is thus seen to exert no special influence on the group score.

d. Possible Influences of Non-Striate Lesions Taken Separately. It has occurred very rarely that a single non-striate cortical field is involved with the destruction of the area striata. Therefore, it is difficult to estimate the possible influences of separate non-striate cortical fields involved. We have divided the animals in each of the cortically operated subgroups into classes according to the non-striate field most involved in addition to the destruction of the area striata. The area of this main additional lesion in each case was measured and expressed as a percentage of the total area of the cerebral cortex. We have computed the average percentage lesion, together with the average error score, for each class. In this way we hope to get some insight into the relative influences of the additional lesions to different non-striate fields upon the class error scores. We are fully aware that the destruction of area striata and the lesser involvements of other non-striate areas than the one in question are not quite uniform in all cases. Table IX presents such a comparison of the class error

TABLE IX

Comparison of the Error Scores of Animals with Additional Injuries to the Various Cortical Fields Besides the Destruction of the Visual Areas for the Inclosed and Open Mazes Which Were Their First Problems

Subgroups IIIa and IIIb were cortically blinded; Subgroups IVa and IVb were both peripherally and cortically blinded. N means the number of cases; M, the mean of the percentage lesions and the mean of the error scores of a special class with a definite non-visual area as the next most involved cortical field. Under "effect" the apparently comparative influences of the additional involvement of the various non-visual fields are indicated.

ANIMAL GROUP	AREAS m'aa (VISUAL ASSOCIATION)			AREA p (AUDITORY)			AREA j (SOMESTHETIC)			EFFECT
	Number	Percentage Lesion	Error Score	Number	Percentage Lesion	Error Score	Number	Percentage Lesion	Error Score	
					Inclosed Maze					
IIIa	6	5.1	885	2	5.8	597	59	2.5	978	j > m'aa > p
	62	4.9	281	18	6.0	379	N = 1	M = 2.5	M = 978.0	
	73	3.8	472	N = 2	M = 5.9	M = 488.0				
	75	4.3	604							
	77	5.7	671							
	80	6.0	636							
	82	5.5	310							
	N = 7	M = 5.0	M = 551.3							
IVa	1	5.0	261	3	5.5	2,725				p > m'aa
	50	5.7	350	20	7.9	524				
	64	5.7	446	22	7.2	1,107				
	85	6.0	630	23	8.9	755				
	90	6.0	2,343	N = 4	M = 7.4	M = 1,277.8				
	N = 5	M = 5.7	M = 806.0							
					Open Maze					
IIIb	15	2.8	1,780	7	7.4	489				m'aa > p
	16	3.8	722	14	7.0	810				
	68	3.8	250	17	5.1	247				
	83	5.3	166	21	7.7	501				
	84	6.0	248	79	6.8	144				
	N = 5	M = 4.3	M = 633.2	87	5.1	211				
				N = 6	M = 6.5	M = 400.3				
IVb	12	6.0	1,122	4	7.8	2,117				p > m'aa
	13	6.0	897	66	7.4	1,645				
	65	6.0	886	67	6.8	716				
	89	5.7	343	69	7.0	702				
	N = 4	M = 5.9	M = 812.0	N = 4	M = 7.3	M = 1,295.0				

scores of the cortically operated subgroups with different chief involvements of the non-striate areas for both mazes which were run as their first problems. With the cortically blinded animals in the inclosed maze, Subgroup IIIa, somesthetic injuries have the greatest influence, although there is only one case in this class; then come the effects of visual association and auditory lesions. With the peripherally and cortically blinded animals in the same maze, Subgroup IVa, the lesions to auditory areas seem to be more influential than those to the visual association areas. This relation is reversed in the relative effects of injuries to auditory and visual association areas with the cortically blinded animals in the open maze, Subgroup IIIb. The auditory lesions are again more influential than the injuries to the visual association areas as judged from the scores of the two classes of the peripherally and cortically blinded Subgroup IVb for the open problem. The relative influence of any main additional non-striate lesion is not at all constant as compared with those of other similar involvements.

The data here presented may be viewed from another angle. The average error score of any class may be substituted for the error score of the subgroup without affecting the position of this subgroup in the error score rankings of the different animal subgroups. For instance, either of the three class error scores of the cortically blinded Subgroup IIIa for the inclosed maze, 551.3, 488.0, and 978.0, may replace the group error score 581.3 and this subgroup still retains its rank between the peripherally blinded Subgroup IIa and the both peripherally and cortically blinded Subgroup IVa. This is generally true of all class error scores of other subgroups for the two mazes. At any rate, our data have not revealed any special distortions of the group error scores by any kind of additional non-striate lesions.

From the controls instituted in the foregoing pages it should be clear that the inclusion of cases with various subcortical lesions or non-striate cortical injuries in computing the constants does not affect significantly the group error scores in any specific direction. In short, the deterioration in the learning ability of the cortically operated groups is mainly the consequence of the removal of the visual cortex.

7. *Some Related Findings*

Before attempting an interpretation of our results we shall turn very briefly to some related findings that have come out in the experimental elaboration of our main theme, even at the risk of some repetition. These accidental findings shed light upon some allied problems and give a hint to the interpretation of our results.

a. Effects of Sense Privation versus Cortical Lesion. Concerning the relative effects of peripheral sense privation and corresponding cortical lesion, the question discussed by Hunter and Lashley, our results are unequivocal in proving that cortical lesion is by far more detrimental. We shall reiterate our findings relevant to this question. Peripheral privation of vision by enucleation of the eyes affects little, if any, the inclosed maze scores; but the extirpation of the visual cortex, even partial, provokes a tremendous retardation (Group V). This is also true of the open maze habit, but to a lesser degree for reasons set forth in the foregoing pages. We shall see presently that the deterioration following the destruction of the visual projection areas is inexplicable by the mere loss of the visual function, for the visual cues are not necessary in the learning of at least the inclosed maze. The detrimental effect must have resulted from the disturbance of some basal function other than visual reception which is much more important for maze efficiency than the visual cues. With the destruction of the visual areas, the loss which counts more is not sensory, but more general. In other words, cortical blinding means loss of this general function as well as that of visual reception. This explains why the cortical lesion to the visual areas is more detrimental than the corresponding peripheral sense privation.

b. Behavior Differences between Normal, Peripherally and Cortically Blinded Animals. Apart from the three criteria of learning, trials taken, time spent and errors made, as adopted in the present study, there is another significant criterion, the quality of the maze performance, of which we are still in need of a convenient standard of judgment. The difference in maze behavior of the normals and the peripherally blinded was hardly noticeable in the inclosed maze; while in the open form the blind animals made more but somewhat reasonable random movements. The cortically operated behaved quite differently from both the normals and the peripherally blinded. Even when they made fairly good learning scores the quality of their work was decidedly inferior to that of the normal controls and the peripherally blinded animals, especially at the initial stage of learning. The cortically operated, even those with only a lesser lesion in the area striata, more frequently wasted their time in the starting box or platform; entered a blind runway repeatedly; ran a straight course in the maze, usually the first three sections; retraced from a particular section of the maze to some other section and repeated this error many times; took some blind runways as regular parts of the pathway to the food; rubbed their sides against the maze-wall at definite spots; or finally, dashed into a certain blind alley and fell asleep, giving up the task entirely. Defaecation and urination in the open maze were other features in the cortically operated. Generally speaking, the differences in maze behavior of the animal groups were more pronounced in the open than in the inclosed maze.

These behavior differences in maze performance, though not capable of quantitative statement at present, are exceedingly important, as they shed light on the way in which the cortical lesion influences the maze efficiency. In a word, the behavior peculiarities of the cortically operated animals are nothing short of symptoms of general dementia, i.e., the defective functioning of the cerebral integrating machine.

INTERPRETATION AND DISCUSSION

Enough evidence has been cited in the foregoing pages to show that the destruction of the visual cortex is more detrimental than the removal of the eyes. And this is generally true for both the inclosed and the open maze habits. It is firmly established in the higher mammals that the visual area is the most specialized of all sensory projection areas of the cortex; a point-to-point correspondence has been found between the retinal quadrants and the visual projection parts in the occipital lobes. The afferent visual system from the retinal beginnings to the cortical terminations is "spatially" organized according to the principle of localization. The same may be said of the visual system in the rat according to Lashley's most recent studies ('34). How can we account for the disproportionate retardation following the loss of the "cortical retinae" (Munk, '81), as compared with that following the removal of the peripheral retinae?

There seems to be three possible explanations, as stated in a preceding section. *1*, the sensory loss other than visual; *2*, the disturbance of visual organization other than the primary sensory functions; *3*, the disturbance of some unknown and non-sensory function of the visual area which may correspond to the *action commune* of Flourens or the non-specific dynamic function of Lashley.

(1) Hunter ('30) interprets the greater defect after cerebral lesions as largely due to the involvement of other sensory areas than the one in question. In a former section we have instituted various controls for our data on the defects of cortical blinding as to the possible influences of additional non-striate lesions. We have treated the possible effects of additional non-striate involvements as a whole and separately. In no case have we found the additional injuries exerting any influence in a special direction. Among the cortically blinded groups, either that with or that without non-striate lesions may represent the whole without affecting its original rank among the normal and operated groups. The influence of any chief additional non-striate lesion is not constant in relation to other similar involvements. The average error score of some animals with a certain dominant non-striate lesion may replace the group score without altering the former place of the whole group in the rankings of the various groups of animals. Finally, it is doubtful that the lesions extending beyond the striate area invaded any other primary sensory area. We are, therefore, forced to attribute the greater retardation of the cortically operated mainly to the loss of visual areas, which constitute the greater part of the cortex involved in the lesions.

Turning once more to facts, our view is strongly supported by the learning scores for the inclosed maze of the partially cortically blinded Group V (Tables III, V and VII). With this group the operation was limited within the area striata or approximately so, without subcortical lesion of any kind. We examined the condition of the non-visual thalamic nuclei for each case to check up any possible involvement of other non-visual cortical areas. All cases in which any of these nuclei showed signs of degeneration were accordingly discarded. In each of the thirteen cases in this group a considerable portion of the visual areas was undoubtedly left functional. Yet this group was far inferior to the peripherally blinded Subgroup IIa in maze efficiency. We reproduce their error scores below:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Inclosed maze, first	120.45 ± 30.01	197.17 ± 47.41
V (Partially cortically blinded)	Inclosed maze, only	317.62 ± 36.70	

Group V, though cortically blinded only partially, made much more errors than the total blind Subgroup IIa. The former also spent more time and took more trials than the latter. The percentage retardations of Group V for the three criteria of learning are fairly constant, a little more than two hundred per cent, with an average retardation of 221.11 per cent, as against the 4.18 per cent of Subgroup IIa. In other words, partially cortically blinded animals are fifty-two times poorer than the peripherally blinded in the same maze. Subgroup IIa made a record of straight success, but the percentage failure of Group V ran as high as 61.54. It seems safe, then, to state that the loss of the visual areas is chiefly responsible for the greater retardation of the cortically blinded animals.

(2) Granted that the extirpation of visual areas entails a greater retardation in the cortically blinded, this fact might still be interpreted as due to sensory disturbance. We started to train our animals at an adult age. It is quite possible that our animals may have developed a spatial organization in visual terms (visual

imagery, if you will). This organization, if present, may survive the loss of eyes and be still functional in maze learning of animals peripherally blinded. Interference with this space system consequent to the destruction of area striata and cortical tissues adjacent to it may affect the maze performance. In such a case, the loss after extirpation of visual cortex would be visual, though not primarily sensory.

This interpretation may be dismissed on experimental grounds. In another experiment just concluded, that is, the third step in our experimental procedure mentioned at the beginning of the present report, we employed animals blinded in infancy before the eyes opened naturally. The visual cortex was thus prevented from functioning visually from birth. The animals thus blinded were not very inferior to the normal controls in the acquisition of the inclosed maze habit and retained the habit very well after a period of two weeks. On the other hand, those animals with additional lesions to the visual cortex learned the maze with difficulty, if at all; and lost the habit heavily after the additional operation, in case the maze had been learned before. The poor scores of these animals cannot be interpreted as due to the loss of the visual function of the visual cortex, as it had never been functioning in a visual way. This constitutes a more decisive proof of the non-visual function of the visual cortex. Since we shall report this experiment in a separate paper, suffice it to mention the main points of our results.

(3) The only alternative left is to attribute the greater retardation after cortical operation to the loss of some non-sensory function of the visual areas. As stated at the formulation of this research program, if the function of the visual areas is purely sensory, as the literary expression "cortical retinae" implies, the loss in maze efficiency after cortical blinding should be comparable to that following peripheral blinding. We found that peripheral blinding has but little influence on the maze performance, especially the inclosed type, while cortical blinding produces much greater retardation than the peripheral operation. The serious deterioration of the cortically blinded is certainly not explicable as merely due to the elimination of the cortical sensory

reception as such. Granted that the visual areas function exactly as "cortical retinae," in the same sense as the peripheral retinae; then their partial destruction means naturally partial blinding. We are reasonably justified in expecting less retarding effect of the partial than the total blinding. But as a matter of fact, the partially cortically blinded Group V was found fifty-two times poorer than the totally peripherally blinded Subgroup IIa in the inclosed maze. On the purely sensory view of the functions of the visual areas, we would be forced to the absurd position of maintaining that partial blinding has even greater retarding influence than total blinding.

The evidence thus seems to preclude a sensory loss, either at a primary receptive or perceptual level, as an explanation of the inferiority of animals with cortical lesions. What the additional function of the striate area may be, which is responsible for the better performance of blind animals with the area intact, is still obscure. The results of our later experiment with blinding in infancy indicate that the function disturbed is not one acquired as a result of visual experience. It may be that the striate area has some innate specific function concerned with the organization of spatial habits and that this specific function is destroyed in the cortically blinded cases. The alternative to such a mysterious function would seem to be some general facilitative function common to this and other areas of the cortex. The results of Lashley ('29) and of Lashley and Wiley ('33b) indicating that a similar condition prevails in each of the sensory fields of the cortex lend strong support to the latter interpretation.

As we see it, the visual areas are normally participating in the integrative activities of the cerebrum as a whole. In the cortically blinded animals, along with the privation of the "cortical retinae," the smooth working of the total neural mechanism is disturbed. It runs at a low ebb and no longer functions in a unitary way, which is required for an efficient maze learning. The operation is local, but its effects are general. Animals thus operated present a picture of dementia. We have some factual support for this statement on the behavior side. With an intact brain, peripherally blinded animals behave as well as the normals in the maze. On the other hand, the cortically operated, even with comparatively light lesions and with the residual visual tissues still functional, betray many behavior peculiarities as enumerated in a preceding section. Enucleation of the eyes results merely in visual anesthesia, while the removal of the visual cortex means general dementia as well. The cerebral integrating mechanism can never function normally in a unitary way without the participation of its visual parts. The function of the visual cortex in this connection is certainly non-visual.

This more dynamic concept of the function of the visual cortex has some parallels in the literature. Munk ('81, '09) produced "psychic blindness" in the dog by inflicting a slight injury to what he called the "cortical retina." Goltz ('81) reinterpreted his results and ascribed them to the "visual weakness" and dementia of the animals. Munk himself noticed that the cortically blinded dog lost orientation to his environment; while the peripherally blinded got readily accustomed to the new situation. Luciani and Seppili ('86) provoked partial psychic blindness in the dog with occipital lesion; the dog reacted to food but failed to distinguish it from other things. Minkowski ('11) extirpated both striate areas in the dog; the resulting disturbance of orientation was far more severe than that in the peripherally blinded animal.

The studies on aphasic defects of Marie, Moutier, Head and others point to the fact that apart from the sensory defects associated with lesions to definite cortical areas, the general intelligence of the subjects suffers even more profoundly. Among the chief symptoms of occipital gun-shot wounds analysed by Poppelreuter ('17, '23), Fuchs ('20, '21) and Goldstein and Gelb ('20) is the hypofunction of "attention." It expresses itself in the inability to count objects visually; in the difficulty in searching for something in the field of vision; in the reduced number of objects grasped at a single glance; in the over-estimation of time interval; in the disturbance of cutaneous localization, and in various other ways. Another notable symptom of occipital lesions is the disturbance of "recognition" or "memory" in general. Poppelreuter found the process of recognition in his patients much slowed down. Heidenhain ('27) and others reported cases who could identify simple familiar things, but not complex ones. Their pattern vision was good enough for perceiving forms, but they were unable to name objects. Here the difficulty lies in the incapability to translate visual impression into verbal terms. The occipital cases are generally unable to interpret visual figures unless more details are given. Poppelreuter is of the opinion that the defect is not merely the loss of visual memory as such but really the inability to see the relations between the separate parts. From his extensive studies of cases of occipital lesions Goldstein ('24) has come to the conclusion that while isolated disturbances of simple sensory functions may occur, there is always some involvement of the entire cerebral mechanism.

We are then forced to conclude that the visually specialized cortical areas have some general function,—an *action commune* in addition to their *action propre,* in the terminology of Flourens. This is a further confirmation of Lashley's analysis that "not only is there diversity in the modes of action of different parts of the cortex but a single area, highly specialized and differentiated for one activity may be wholly undifferentiated with respect to another in which it also participates." (Lashley, '31c). This general function, perhaps common to all specialized cortical areas, is probably instrumental in bringing about the unitary functioning of the brain as a whole.

Another point waits for some comment. The dispensability of vision for the inclosed maze is by no means absolute. It is unnecessary for animals with normal brains, but not for those with a brain deprived of the visual areas. How can we account for the different rôles which vision plays in the two cases? There seems to be only one possible explanation. First, the removal of the eyes has no influence on the learning of the inclosed maze. If visual cues are normally used the blind animals have no difficulty in falling back upon the non-visual cues. As pointed out by Lashley ('29) the sensory elements of the maze habit may have an alternative function, so that the elimination of one sensory system would be followed by the performance of the habit through the use of other undisturbed sensory cues. With the open maze habit this transfer cannot be effected without much loss of efficiency. Second, the destruction of the visual cortex has serious influences on learning. As demonstrated before, this cannot be the consequences of the abolition of a sensory function, since vision is not necessary for learning the maze at normal rate. The detrimental effect in this case is primarily due to interference with the functional efficiency of the rest of the nervous system or to the defect of the associative mechanism. Third, the elimination of the eyes in animals with injuries to the striate areas produces additional retardation, although it has little or no effect on animals with normal brains. In all probability, animals with striate lesions still use some brightness cues: the loss of eyes leaves them without these cues and they somehow have greater difficulty in falling back upon non-visual cues. The visual areas normally participate in the general integrative activity of the cerebrum; with their privation the cerebral mechanism ceases to be an unitarily functioning affair. It loses much of its function as an agent to adjust different nervous processes to do a certain task, thus unifying the bodily functions. With the mutilated integrating mechanism an alternation of the sensory components can no longer be readily effected, as in the case of animals with normal brains. In other words, the greater difficulty of readjusting the sensory components of the maze habit in cortically operated animals is to be attributed to the mutilation of the cerebral integrative function, that is, to general dementia.

SUMMARY AND CONCLUSIONS

Animal groups, normal, blinded peripherally, cortically and in both ways have been trained in inclosed and open mazes of the same pattern with the following results.

1. The open maze is easier than the inclosed for normals and possibly for the cortically blinded, but more difficult for the total blinds whether or not with additional cortical blinding.
2. The removal of the eyes has little or no influence on the learning of the inclosed maze, but has tremendous effect on the learning of the open maze.

3. The destruction of the visual projection areas is more detrimental than the removal of the eyes. Cortical lesion is more detrimental than the corresponding peripheral sense privation. This is true for both forms of the maze.

4. After the destruction of the visual areas the animals still retain some position and brightness vision, but the pattern vision is all gone.

5. The residual vision is more important for the learning of the inclosed maze by the cortically blinded animals than is the case with normal controls.

6. In the absence of pattern vision in the cortically blinded animals, the residual vision seems to be able to supply visual cues for the general orientation and consequently for the better performance in the open maze.

7. Peripheral blinding when combined with cortical blinding produces further retardation, the effect being greater in the open than in the inclosed maze habit.

8. The additional retardation, just mentioned, is explicable by the greater difficulty in falling upon non-visual cues than is the case with the peripherally blinded animals with normal brains; this in turn is due to the defective cerebral integration.

9. Vision always plays a greater rôle in the open than in the inclosed maze habit, irrespective of the working condition of the cerebral mechanism.

10. The quality of maze performance of the cortically blinded is inferior to that of the peripherally blinded and the normals, suggesting dementia in the cortically operated.

11. The visual projection areas normally participate in the integrative activity of the cerebrum as a whole; that is, in addition to their primary function of visual reception, they still have some sort of a general function.

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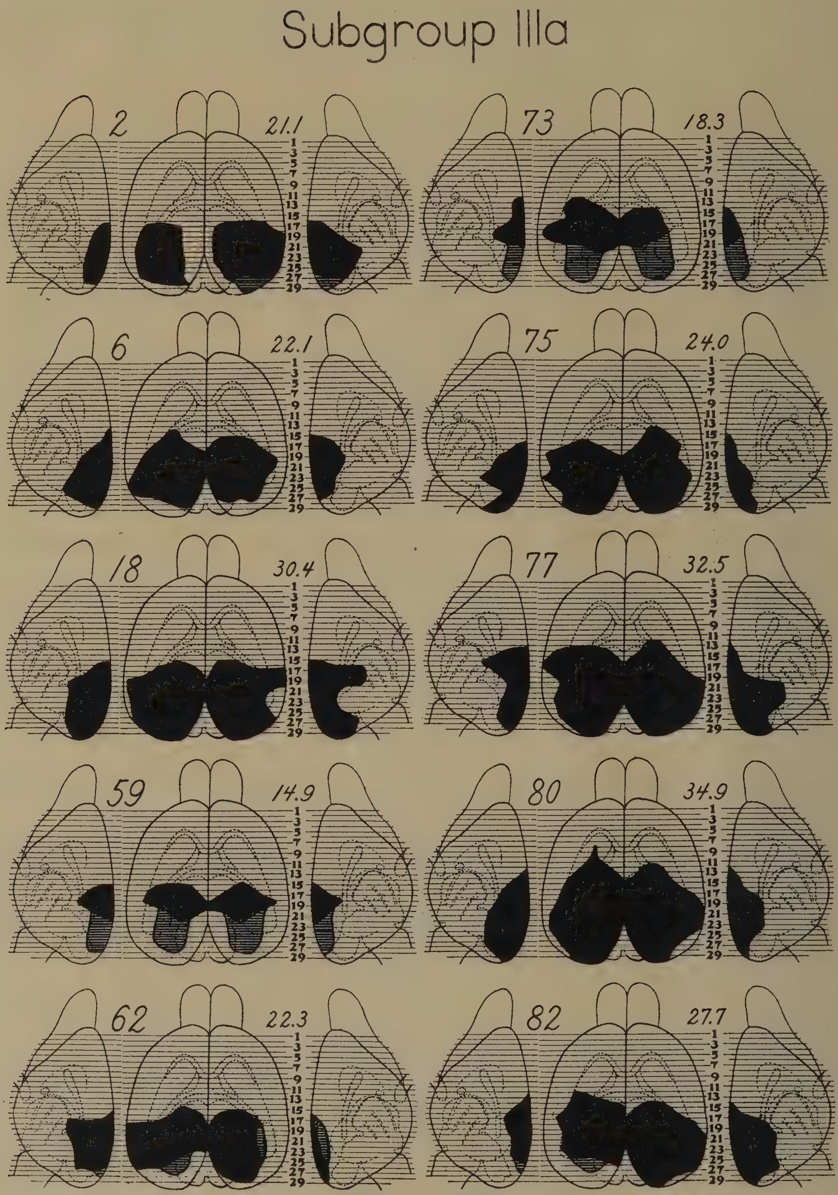
PLATES

Diagrams of the Extent and Locus of the Cerebral Lesions in Each of the Animals Reported in This Study

In those parts marked with heavy transverse lines traces of visual tissue were found but probably unfunctional. The cerebral lesions in Group V were less extensive, only dorsal views of the reconstructions being given. For each diagram, the figure at the left is the identification number of the case used in the tables and the text; that at the right, the percent age of the cortex removed.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59
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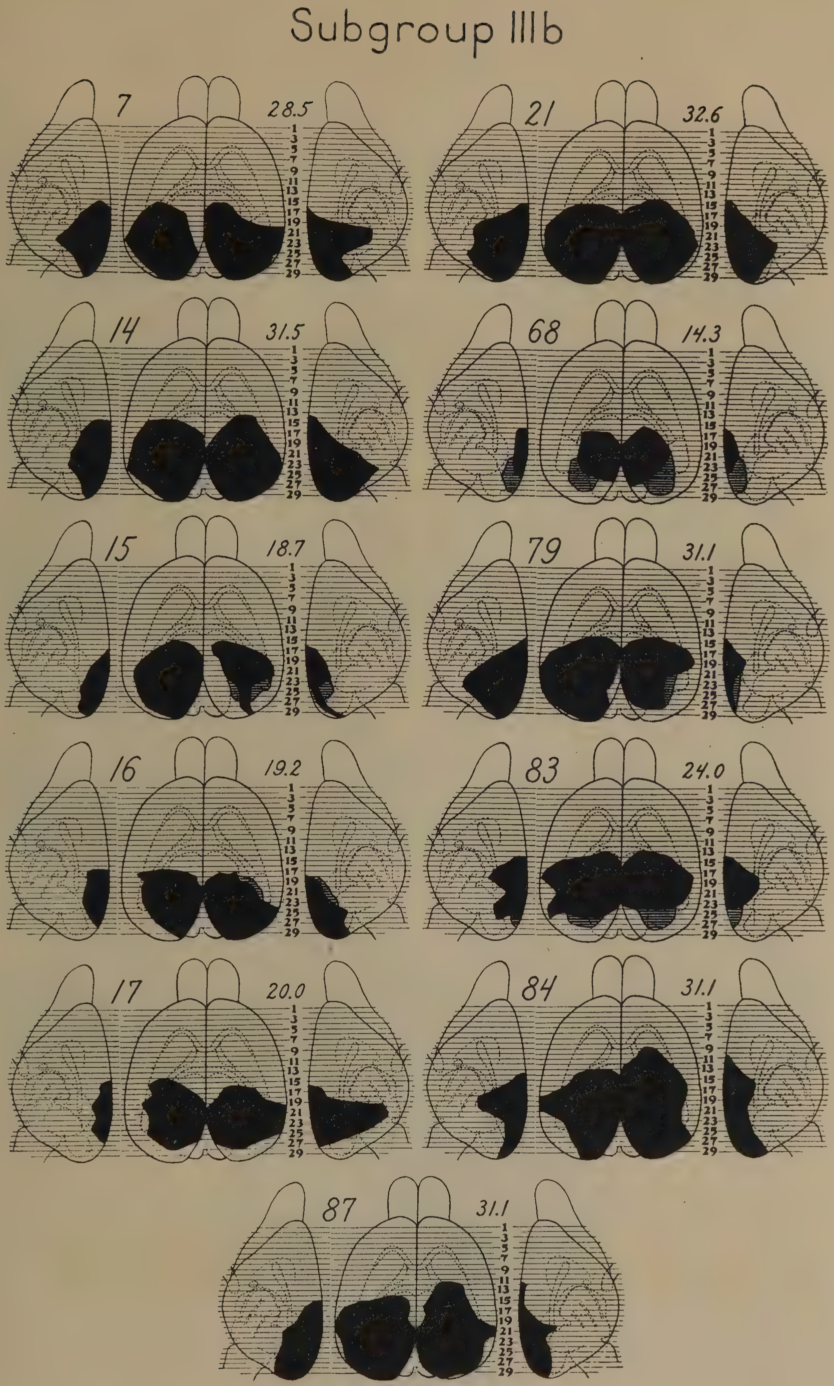
80
34.9
62
22.3
82
27.7
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29

PLATE 1

Subgroup IIIa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24.0
17
20.0
84
31.1
87
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13
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17
19
21
23
25
27
29

PLATE 2

Subgroup IIIb

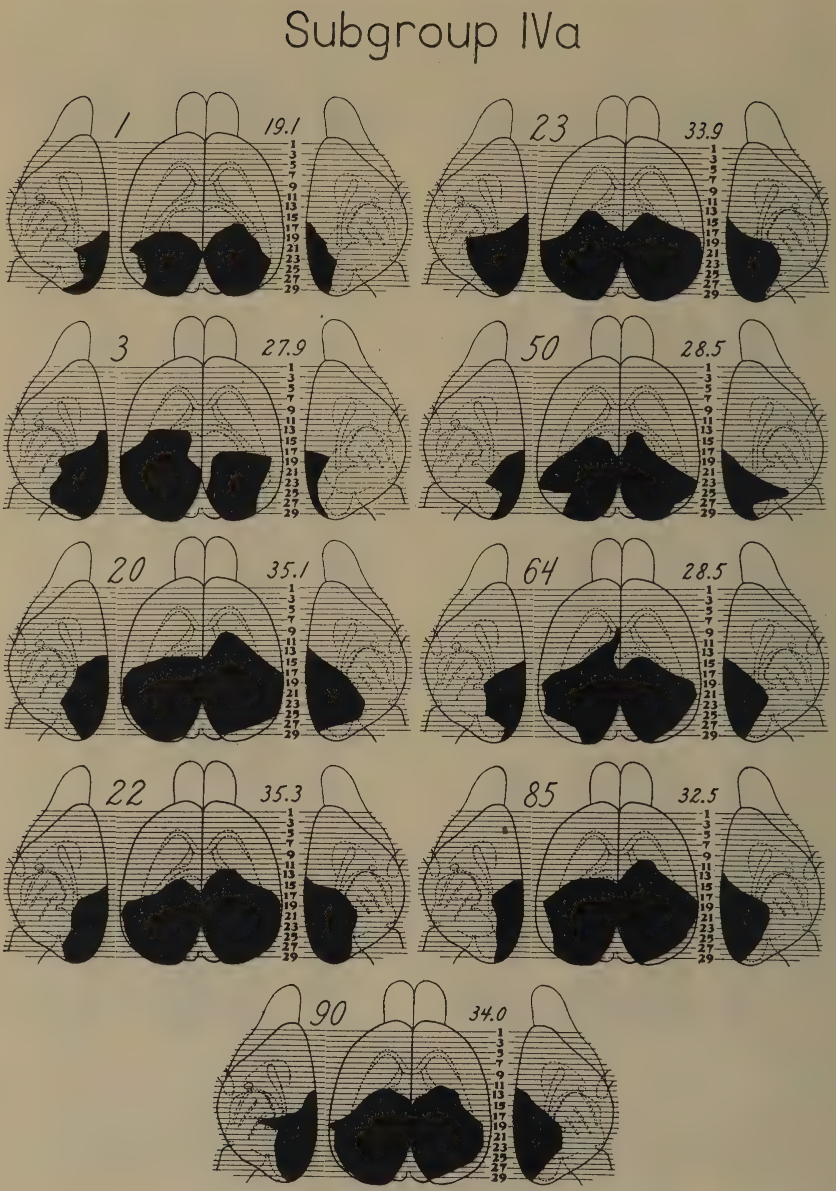
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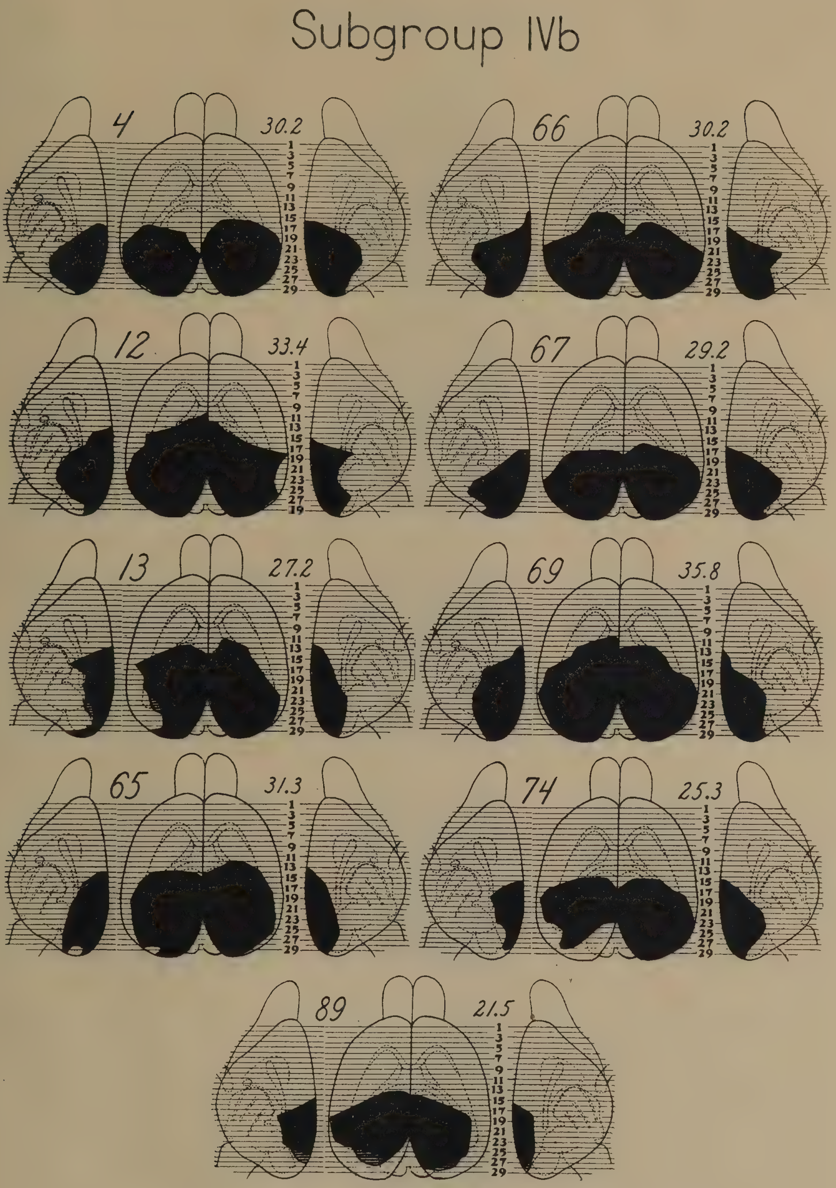
PLATE 3

Subgroup IVa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29.2
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35.8
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31.3
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21.5
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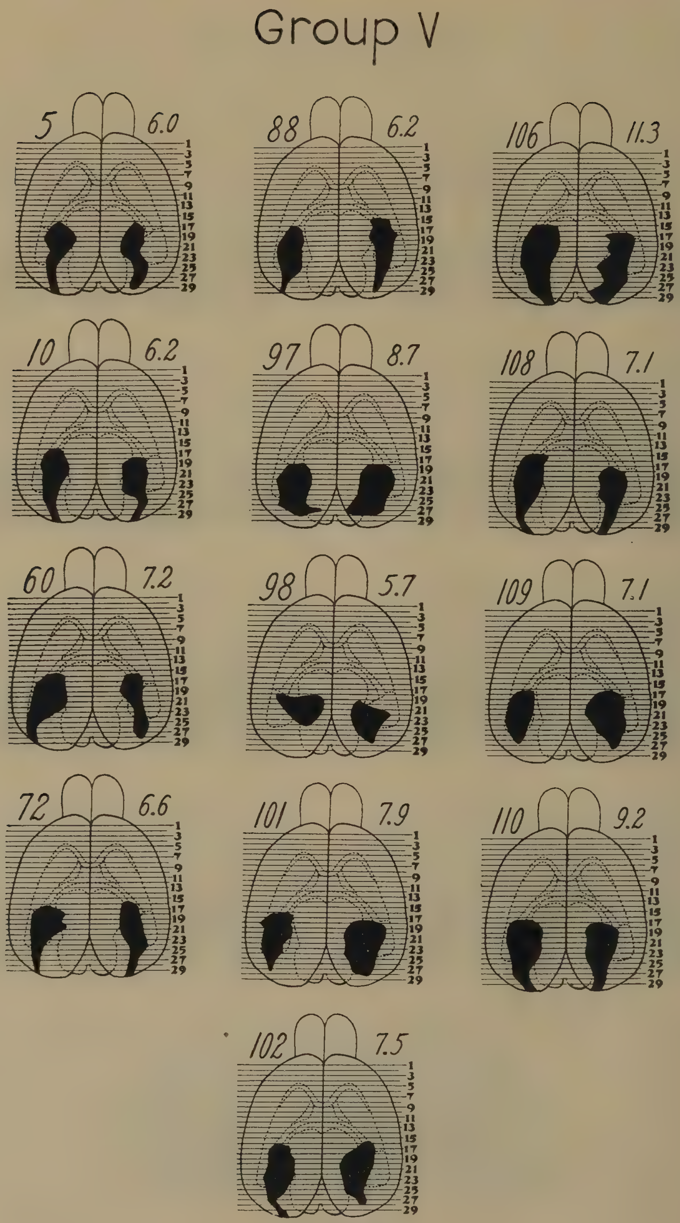
PLATE 4

Subgroup IVb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98 5.7
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72 6.6
101 7.9
110 9.2
102 7.5
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29

PLATE 5

Group V

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